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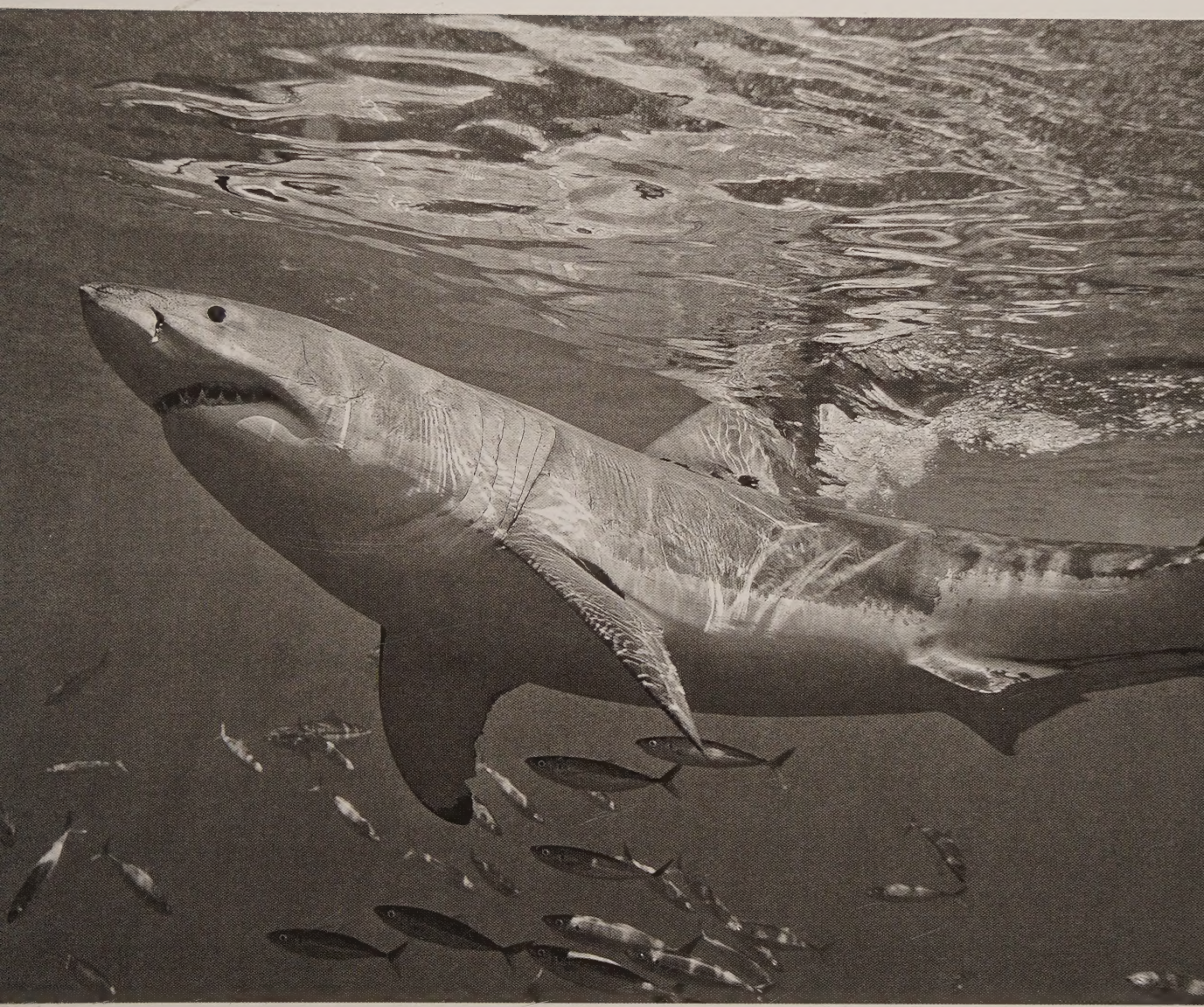

White Shark

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Marine Fisheries REVIEW

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On the cover:
Young white shark, *Carcharodon carcharias*, at Isla Guadalupe, Mexico.
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Articles *78(1–2), 2016*

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Methods for the Preparation of Pacific Spiny Dogfish, *Squalus suckleyi*, Fin Spines and Vertebrae and an Overview of Age Determination

CINDY A. TRIBUZIO, MARY ELIZABETH MATTA,
CHRISTOPHER GBURSKI, NIKKI ATKINS, and WALTER BUBLEY

Introduction

Age determination of elasmobranchs presents unique challenges compared to that of teleosts. Elasmobranchs do not have calcareous otoliths or scales, structures commonly used to age teleosts. Various techniques, including bomb-radiocarbon dating, histological staining, and X-radiography, have been applied to hard structures such as fin spines, vertebrae, and caudal thorns to age elasmobranchs (Cailliet and Goldman, 2004; Carlson and Goldman, 2006).

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To be viable for an age determination study, a hard structure must form visible, annually-formed growth patterns. Typically, these growth patterns consist of alternating light and dark bands; each pair of growth bands is termed an "annulus," representing 1 year of growth. Note that this differs from the standard English definition of the word annulus, which is derived from the Latin word "anus" meaning "ring," not "annus" meaning "year" (Panfili et al., 2002).

In most elasmobranch studies, sagittally sectioned vertebrae are selected as the primary age structure (Cailliet and Goldman, 2004), although clarity of annuli within vertebrae is largely species-specific. For some species, vertebra growth patterns are not discernible and thus alternative structures such as the neural arch (McFarlane et al., 2002) or dorsal fin spine (Clarke and Irvine, 2006) must be used.

Squaliform sharks (dogfishes) are one of two orders of elasmobranchs possessing dorsal fin spines (Clark and Irvine, 2006). Pacific spiny dogfish, *Squalus suckleyi* (hereafter termed "spiny dogfish"), is a species of Squaliform shark found throughout the North Pacific Ocean, ranging from the Koreas and Japan through Russian and Alaskan waters to the North American west coast, reaching as far south as Baja California (Ebert et al., 2010). *Squalus suckleyi* was previously thought to be identical to its Atlantic counterpart, *S. acanthias*, but genetic, meristic, and morphological evaluation has proven them to be two distinct species (Ebert et al., 2010). Further, *S. suckleyi* differs from *S. acanthias* in several key life history attributes, including slower growth, larger maximum size, and later maturity. Much of the existing scientific literature from the North Pacific Ocean refers to spiny dogfish collected there as *S. acanthias*, and it is important to note that the species name is now considered incorrect in previous literature and should be considered *S. suckleyi*.

The dorsal fin spine method has been used to age *S. suckleyi* and *S. acanthias* since the 1930's. In this method, annuli on the enamel of the second dorsal fin spine are viewed and counted using reflected light and a dissecting microscope or with image analysis software. However, this may not be the best method to accurately describe age and growth of the species. Because the dorsal fin spine extends from the body into the environment, breakage and erosion of the fin spine often occurs over time. Thus, larger, older spiny dogfish tend to have fin spines with more wear than smaller, younger fish.

Ketchen (1975) developed an algorithm to estimate the number of missing annuli in the worn portion of the fin spine using the relationship between the enamel base diameter and the number of annuli counted on un-

ABSTRACT—The Pacific spiny dogfish, Squalus suckleyi, *is a small shark species commonly found in the North Pacific Ocean. Age determination for this species has historically been conducted by examination of the dorsal fin spine with little change in methodology since the 1930's. Despite extensive use, there are two major caveats associated with fin spines as age structures: 1) fin spines protrude from the body and are subject to damage, requiring estimation of annuli contained in missing portions of the fin spine and 2) there is a high degree of inter- and intra-reader variability due to difficulty in interpreting fin spine growth patterns. A new method was recently developed for* S. acanthias, *a North Atlantic Ocean congener of* S. suckleyi, *using histologically stained thin sections of vertebrae instead of dorsal fin spines for age estimation. Here, we apply this histological method to vertebrae of* S. suckleyi *and describe the historic methodology for dorsal fin spines. This document presents detailed procedures for both methods, including sample collection, sample preparation, and age estimation criteria for each structure.*

worn fin spines. An alternative analytical method for estimating lost annuli was proposed by Cheng (2012); however, few laboratories have adopted this method to date.

Taylor et al. (2013) conducted a detailed examination of the Ketchen and Cheng analytical approaches and determined that both methods produced questionable age estimates for larger, older fish, and they further recommended an examination of new methods. Attempts to improve Ketchen's algorithm (McFarlane and King, 2009) have not addressed problems of error from other sources (e.g., natural variability, reader error); therefore, the historical method continues to be used (Tribuzio et al., 2010).

Fin spine-based age estimates of both *S. suckleyi* and *S. acanthias* have been validated using bomb-derived radiocarbon (Campana et al., 2006). Furthermore, annual periodicity of the fin spine banding pattern has been verified by oxytetracycline (OTC) injections and tag/recapture methods on *S. suckleyi* that were at liberty up to 21 yr (McFarlane and Beamish, 1987; McFarlane and King, 2009). However, the low precision of fin spine-based age estimates (CV = 19%; Rice et al., 2009; Tribuzio et al., 2010) is problematic, and systematic bias among age determination laboratories occurs despite age validation (Rice et al., 2009). Measurement errors among readers, potential systematic errors among laboratories, and process errors associated with estimating the number of worn annuli all combine to produce the low precision in age estimates and therefore growth parameters (Tribuzio et al., 2010). This error has ramifications for population modeling and biological reference points for fishery management (Tribuzio and Kruse, 2011).

To address these issues, a new method of age determination using vertebrae has been developed for *S. acanthias* in the northwest Atlantic Ocean (Bubley et al., 2012). This method employs histologically stained vertebra thin sections and presents two advantages over the old dorsal fin spine method. First, vertebrae do not wear or break over time as fin spines do, therefore reducing one source of variability and error in the age determination process (i.e., the need to use a modeled estimate for the number of missing annuli in worn fin spines). Furthermore, age estimates derived from vertebrae are far more precise than those from spines (Bubley et al., 2012).

Results are not presented in this paper as it is intended solely as a technical guide for the collection, laboratory processing, and interpretation of age structures. This paper is part of a larger spiny dogfish age determination project. While both methods are presented here to improve precision and document ageing criteria for use by other laboratories, it is important to note that at this time, the vertebra method does not appear to be appropriate for older spiny dogfish (Tibuzio et al., in press). Documenting age determination methods is imperative, as criteria used for identifying annuli can drift over time and among agencies. This paper provides a central reference for all laboratories involved in spiny dogfish age determination and will promote consistency between the two methods and among spiny dogfish age readers, in the hopes of improving inter- and intra-laboratory precision.

Sample Collection

Squalus suckleyi is a small shark with medium-brown to gray coloration dorsally and white ventrally; white spots are often present along the upper body. A prominent spine is present along the anterior edge of each dorsal fin. A complete description of identifying characteristics is available in Ebert et al. (2010). While there are at least 25 species of the genus *Squalus* occurring throughout the world, *S. suckleyi* is the only one occurring in the eastern North Pacific Ocean. However, the species can be confused with members of the Triakidae family (e.g., brown smoothhound, *Mustelus henlei*), which possess an anal fin and do not have dorsal fin spines. In the western North Pacific Ocean, *S. suckleyi* may overlap with other *Squalus* species near the far southwestern edge of its range, in particular, *S. japonicus*, *S. blainville*, and *S. brevirostris*. However, *S. suckleyi* is generally easy to distinguish from the other *Squalus* species because of the white spots along the sides and because the origin of the first dorsal fin spine is posterior to the rear free tips of the pectoral fins, whereas in most species of *Squalus* occurring in the western North Pacific Ocean the first dorsal fin and spine are located above the pectoral fins (Compagno, 1984).

The first steps in spiny dogfish collection are to sex and measure each fish. Sex can be determined externally; males have paired claspers attached to the pelvic fins. Special care may be needed when identifying sex of very small (immature) animals, as male claspers can be small. There are four commonly used length measurements for spiny dogfish (Tribuzio et al., 2009), measured from the tip of the snout to 1) the dorsal pre-caudal pit (pre-caudal length, PCL); 2) the deepest indentation of the tail fork (fork length, FL); 3) the dorsal tip of the tail in its natural position (natural total length, TL_{nat}); and 4) the dorsal tip of the tail with the upper lobe of the caudal fin depressed to align with the horizontal axis of the body (extended total length, TL_{ext}) (Fig. 1). However, PCL has the least amount of measurement error and is often the easiest to measure. This is the preferred length measurement for the species, but equations exist to convert among length measurements (Tribuzio et al., 2009; Tribuzio and Kruse, 2012).

Two age structures are collected: 1) the posterior dorsal fin spine (hereafter termed "spine" and 2) a section of the vertebral column. The posterior spine is preferred to the anterior spine because it is larger and generally subject to less wear. Vertebra samples can be collected at various positions along the vertebral column. The authors have found that vertebrae collected more anteriorly are generally larger, making them easier than posterior vertebrae to prepare and read. If time allows, it is preferable to collect vertebra samples ventral to the anterior dorsal fin;

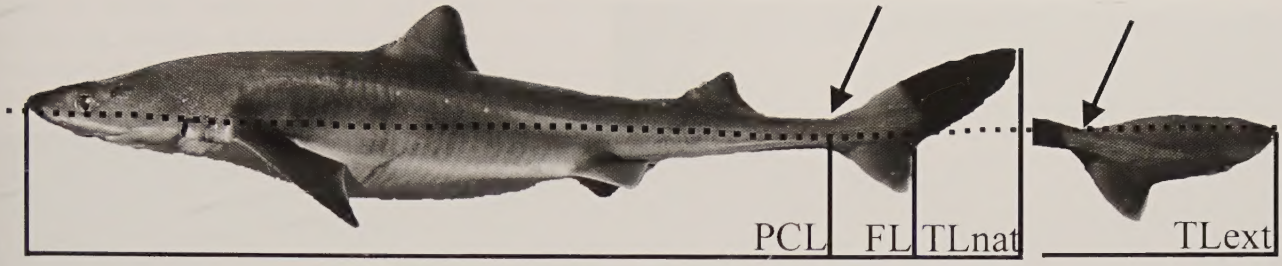

Figure 1.—External measurements for spiny dogfish. All measurements start at the snout and extend to either the pre-caudal length (PCL), fork length (FL) or total length (TL, both natural and extended). The dashed line shows the horizontal axis of the body for measuring TL extended). For this sampling plan only the PCL is used. The arrow points to the pre-caudal notch. From Tribuzio et al. (2009).

however, it is quickest to collect the vertebrae and posterior spine simultaneously (Fig. 2).

For collection, a vertical incision is made behind the posterior spine, slicing down (ventrally) through the vertebral column (Fig. 2A). Then an incision about 4 inches long is made horizontally towards the head, keeping the blade ventral to the vertebrae (Fig. 2B). The section is removed by cutting vertically to the dorsal side (Fig. 2C). Excess muscle tissue should be trimmed to make storage easier (Fig. 2D, 2E). Samples should be stored in individually labeled, single-specimen reclosable bags and frozen. Vertebra and spine samples from the same animal can be stored in the same bag. The same cutting and sample storage/preservation method can be used regardless of whether the vertebra samples are removed from the anterior or posterior portions of the vertebral column.

Specimen Preparation

Dorsal Fin Spines

Various techniques and tools can be used to prepare spines for age determination. The frozen spines and vertebrae need to be separated and the vertebrae retained for further processing as described in the next section; it is advisable to do this with the structures frozen or partially frozen to prevent tissue degradation of the vertebrae prior to processing.

Spines need to be heated to aid in tissue removal, taking care not to damage the spine enamel or base structure. Heating will create a strong odor and it is recommended to use a well-ventilated area or to process under a fume hood. Spines may be heated either using a microwave or hotplate. To microwave, spines should be placed, either individually or as batches if each is in an individually labeled microwave-safe bag, in a microwave-safe container filled with water. If spines are in individual bags, the bags should be punctured to allow water to flow through. Depending on the power of the microwave, the size of the container, and the number of spines, it should only require 2–6 min to adequately heat the spines. Alternatively, spines may be heated in large, water-filled beakers or in a divided basket within a large tray placed on a hotplate for several minutes. Tissue should easily scrape off the surface of the spine with gentle rubbing.

Tools that are helpful for cleaning the inner surfaces of spines include forceps, microprobes (i.e., dissecting needles), and dental picks. For cleaning the outer enamel, the best tool is a fingernail; however, a soft toothbrush (used gently) or a cloth can be useful. Metal tools should be used with caution on the outside of the spine because they may damage the enamel surface used for age determination.

All soft tissue needs to be removed from the exterior and interior of the spine. While working on a spine, it is helpful to keep the spine wet, otherwise the tissue becomes sticky and difficult to remove. The outside of the spine can be initially cleaned by carefully scraping away the tissue with a fingernail or other soft tool. Remaining tissue on the exterior of the spine can be carefully removed with forceps or another fine-tipped tool. The cartilage plug on the inside of the spine will generally slide out as one piece and can be pulled out with forceps or a dental pick. Once the plug is removed, any tissue remaining inside the spine can be scraped away without concern of damage to the interior of the spine.

Spines can be stored long term in individual paper coin envelopes. After cleaning, each spine should be allowed to air dry for at least 24 h to eliminate all moisture and potential sources of decay and to prevent the spine from sticking to the paper storage envelope. Spines may become brittle after many years of storage, so care is warranted when handling archived envelopes. Some laboratories use a barcode system to track samples; if this is the case, the barcode sticker can be placed inside the envelope just below the fold of the envelope's flap. Barcodes can still be scanned from this location, and if the adhesive weakens, the barcode label will not be lost.

Vertebrae

To prepare spiny dogfish vertebrae for age determination, they must be individually dissected, thin-sectioned, stained, and mounted on glass slides. Histological staining methods have been adapted from Bubley et al. (2012). Supplies needed to prepare

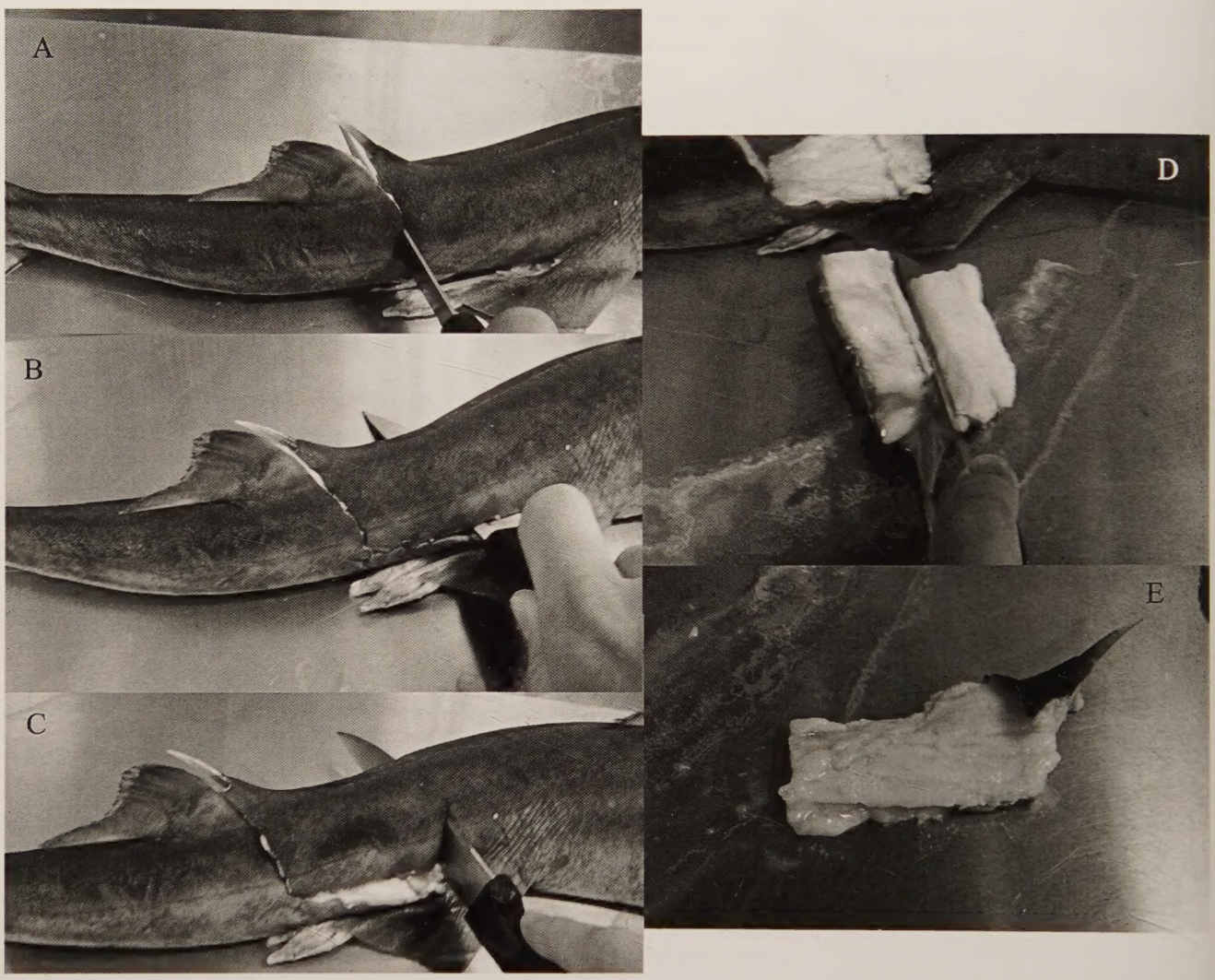

Figure 2.—Dorsal fin spine and vertebrae dissection. A) A downward incision is made posterior to the dorsal fin spine, followed by B) a horizontal incision ventral to the vertebral column, and finally C) an upward incision is made to simultaneously remove the spine and a portion of vertebral column. D) Excess tissue is removed from the spine and vertebrae to produce E) a single sample ready to be frozen until further processing in the laboratory is possible.

vertebrae are listed in Table 1. Personal protective equipment such as eye goggles, latex or nitrile gloves, and laboratory coats should be worn when handling chemicals. A chemical fume hood should be used where indicated, and refer to material safety data sheets (MSDS) for proper handling, storage, and disposal of all chemicals.

Dissection

Vertebral column sections must be at least partially thawed before excess soft tissue can be scraped away. Once thawed, a scalpel or sharp knife is used to cut excess tissue from around the vertebral column section. The axial processes (neural and hemal arches) may be left attached to the vertebrae to simplify cleaning, and any remaining soft tissue can then be scraped off with the back of a knife.

Individual centra are separated from the vertebral column using a scalpel. The axial processes and remaining soft tissue can then be trimmed from each centrum. Care should be taken when removing excess tissue from each centrum; fine forceps can be used to remove stubborn tissue. It is often not possible to remove all the tissue; however, this will not impact age determination. Several vertebra centra per animal can then be stored in individual vials containing 70% ethanol to await sectioning and staining. If desired, the remainder of the vertebral column may be stored frozen.

Thin-sectioning

Silicone molds (suggested size: 64 × 70 × 12 mm) are used to encase

rows of vertebra centra in resin for sectioning multiple specimens simultaneously. A brand of resin that works well for this purpose is Polytranspar Artificial Water[1], a clear casting resin that requires a catalyst to harden (available at taxidermy supply businesses). A new batch of resin must be mixed for each use because it starts to harden immediately once the catalyst has been added. Wax cups pre-marked in 2 oz increments are quite helpful for mixing the resin as they can be disposed of once the unused catalyzed resin hardens.

First, working in a fume hood, a batch of resin is mixed and a thin layer is poured into the mold such that it just barely covers the bottom of the mold. The mold should be left undisturbed for about 40 min to allow the resin to harden until tacky. A line should be drawn in the resin, using a probe and a ruler as a guide, for aligning multiple vertebra centra. Either the anterior or the posterior end of each centrum is then pressed into the resin with the focus on the guideline, to result in a longitudinal section. Space should be left at the top of each block to place a label with the specimen numbers for each row. Each block can accommodate 2–3 rows of vertebrae, with 4–7 vertebrae per row.

Once aligned, the vertebrae need to dry in place (about 30 min) so they are held firm in the bottom layer of resin. This prevents the vertebrae from shifting as the top layer of resin is poured. A new batch of resin is then poured over the centra so that they are fully covered while striving to keep block thickness to a minimum. Excess resin can cause difficulties when sectioning. The resin should be allowed to dry a minimum of 2 days in the fume hood.

After the resin is fully cured, vertebrae are sectioned with a high-speed saw such as an IsoMet 5000 (Buehler-ITW, Lake Bluff, IL). Optimal section thickness for spiny dogfish vertebrae is 0.4 mm, although some variation is acceptable as long as stain penetration and annulus clarity are not affected. We recommend checking the thickness of the distal ends of each section with calipers to verify that the saw is cutting accurately. Thin sections can be stored in 70% ethanol indefinitely. Excess resin should be trimmed away from the vertebra sections using a sharp scalpel prior to staining.

[1]Mention of trade names or commercial firms is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1.—Supplies used for sectioning, staining, and mounting vertebra centra.

Sectioning supplies	Staining supplies
Wax cups marked in 2 oz increments	Histology tissue cassettes
Tongue depressors	Large beakers
Strips of paper ~ 1 cm wide (to label blocks)	Graduated cylinders
Dried, cleaned vertebrae	Containers to store reagents
Silicone molds	Funnel
Polyester resin	Glass slides
Forceps	Cover slips
Probe	Slide boxes
Paper towels	Hot plate
Scalpel	Orbital shaker or stir plate with bars
Scissors	Stopwatch
Precision saw with diamond blade	Small and large forceps
Dissecting microscope	Scalpels
Ruler	Flammable chemical disposal container
Calipers	Dissecting microscope
	Plastic tub
	Trays
	Paper towels
	Distilled water
	Modified Harris hematoxylin
	Gelatin
	Glycerol
	Listerine
	Hydrochloric acid (12 M)
	Ethanol (100%)
	RDO Rapid Decalcifier

Solution Preparation

Several of the solutions used to stain and mount specimens can be prepared in advance: acid-alcohol, a series of concentrated glycerin solutions, and Kaiser glycerin jelly. Acid-alcohol, used to destain specimens, is prepared using 65% distilled water, 35% ethanol, and 12 drops of 12M hydrochloric acid per 300 ml water/ethanol mixture. Acid alcohol should not be reused and should be disposed of according to local and federal regulations.

A series of increasingly concentrated glycerin solutions (25, 50, 75, and 100%) is used to hydrate stained thin sections to prepare them for mounting. Distilled water is added to 100% glycerin to make the glycerin solutions (25, 50, and 75%). Each glycerin solution can be stored in a separate container and reused, although the weaker solutions (25 and 50%) are more prone to mold formation and must therefore be changed more frequently.

Kaiser glycerin jelly is used to adhere stained specimens to glass slides and affix coverslips. It is made using 40 ml distilled water, 7 g Knox gelatin, 50 ml glycerol, and 10 ml Listerine antiseptic mouthwash (any flavor which has thymol as an active ingredient). The water and glycerol are mixed together, then sprinkled with the gelatin, and allowed to sit for 5 min. The solution is then melted at low heat using a hot plate or double boiler (gelatin's melting point is 40°C). After the gelatin has dissolved, the solution is removed from the heat and Listerine added, stirring slowly to prevent formation of bubbles. The Kaiser glycerin jelly solution is then allowed to cool until it is completely solid prior to use.

Staining

Vertebra thin sections are placed in histology tissue cassettes labeled with specimen numbers. Multi-chamber cassettes may be used to prepare many specimens simultaneously if desired.

Cassettes are placed in a large beaker on an orbital shaker and fully immersed in RDO Rapid Decalcifier (Apex Engineering Products Corp.). A partially full bottle of water or Erlenmeyer flask may be nested within

the beaker to keep the cassettes submerged. Sectioned vertebrae should be soaked in RDO until softened (flexible) and yellowed. It is recommended to check sections after 5–10 min and re-immerse in RDO if not adequately decalcified. In general, larger vertebra sections require longer soak times, but a total soak time of roughly 15 min is adequate for most specimens. Soaking too long will cause the sections to decalcify to the point where annuli are not visible after staining. Once the specimens are sufficiently decalcified, cassettes are removed from the RDO and placed in a beaker under running water for 1 h. RDO can be reused until precipitates form. Following decalcification, cassettes need to be soaked in 100% distilled water for at least five minutes, although the process can be stopped here overnight.

The following seven steps need to be conducted sequentially, i.e., no overnight breaks. Solutions are placed in a beaker on an orbital shaker to ensure constant movement.

1) Soak the cassettes in modified Harris hematoxylin (Richard-Allen or Thermo Fisher Scientific) for about 8 min. Total soak time may vary depending on size and thickness of vertebra sections, and it is recommended to do some test samples to determine the best soak time to achieve optimal staining. Fresh hematoxylin should be used because this chemical loses potency after expiration. Precipitates may sometimes form within open containers of hematoxylin and can be filtered out using conical paper coffee filters.
2) Rinse the cassettes in a laboratory sink by soaking in multiple water baths until the water runs clear. The staining level should be checked for adequacy by examining sections under a dissecting microscope. Staining should be uniform and dark, and annuli should be visible although contrast between light and dark bands may be low. If additional staining is required, Steps 1 and 2 can be repeated until the desired level of staining is achieved.
3) De-stain the specimens with acid alcohol solution for about 4 min to make the banding pattern more visible and improve contrast between light and dark bands.
4) Place the cassettes in a tub filled with water in the sink and rinse using agitation for about 1 min. Again, check sections under the microscope to ensure de-staining is adequate. A pattern of alternating light and dark bands, purple or red in color, should be evident. If necessary, Steps 3 and 4 can be repeated, although the time spent in acid alcohol may be adjusted based on staining strength.
5) Rinse the cassettes in the sink under running water for 10 min.
6) Soak the cassettes in distilled water for 2 min.
7) Soak the cassettes in gradually increasing concentrations of glycerin: 10 min each in 25, 50, 75, and 100% glycerin. Vertebrae can be left in 100% glycerin overnight if there is insufficient time for slide-mounting.

Specimen Mounting

To mount specimens, a stained vertebra thin section and a small (pea-sized) amount of Kaiser glycerin jelly is placed next to each other on a labeled glass slide. The slide is then placed on a hot plate set to the lowest temperature that will melt the jelly in a period of 30–60 sec. The temperature should be set as low as possible to prevent formation of air bubbles, which can occlude specimens.

Once the jelly is melted, a coverslip is placed over the vertebra. It is best to hold the cover slip at roughly a 30° angle to the slide, touching the jelly, and then slightly drag it towards the specimen, which will cause the jelly to melt around and underneath the specimen when the cover slip is placed on top (i.e., there is no need to move the vertebra on top of the melted jelly).

The slide is then allowed to cool completely. Excess jelly that leaks from under the cover slip should be removed using a razor blade so the slides won't stick together during storage.

Age Determination

Dorsal Fin Spines

As described, accurate age estimation of spiny dogfish spines is difficult because the spines are external to the body and are often broken or worn, resulting in "missing" annuli, the number of which must be estimated using regression methods based on morphometric relationships. Several different measurements taken on each spine (Fig. 3) are used to calculate the number of potentially missing annuli. Measurements can be taken using either calipers or image analysis software, but the method should be consistent for all specimens in a given study.

In the Ketchen (1975) approach, the two key measurements used in estimating lost annuli are the enamel base diameter (EBD) and the diameter at the last readable point (LRP, also called the "no-wear point" and the diameter at this point is LRD) (Fig. 3). For the Cheng (2012) approach, the mid-point measurement (MID) is used in addition to the EBD and LRD (Fig. 3). The MID is somewhat subjective, based on the reader's interpretation of the spine, and represents the location along the spine where the reader feels that the readability of the spine degrades and confidence in the interpretation of annuli decreases. Three additional measurements, total length (TL), stem length (SL), and spine base diameter (SBD) (Fig. 3) can be used for other applications such as determining relationships with animal size; however, they are not necessary for estimating the number of missing annuli.

Further descriptions of the spine reference its orientation in situ (Fig. 4). The enamel on the tip (dorsal edge) is typically the most worn portion of the spine. Wear progresses ventrally from the anterior to the posterior edge of the spine. It is important to accurately identify the LRP, which is the most dorsal point of enamel on the anterior edge (Fig. 5A). The LRD is measured on the enamel between the anterior

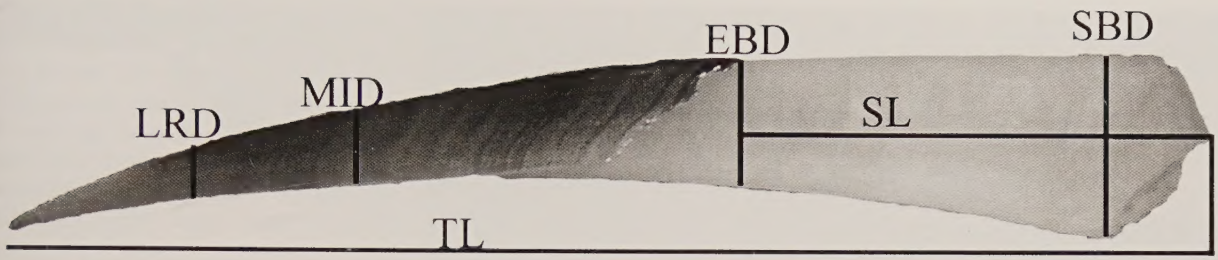

Figure 3.—Measurements taken for each fin spine: LRD=last readable point diameter; MID=mid-point diameter; EBD=enamel base diameter; SBD=spine base diameter; SL=stem length; TL=total length.

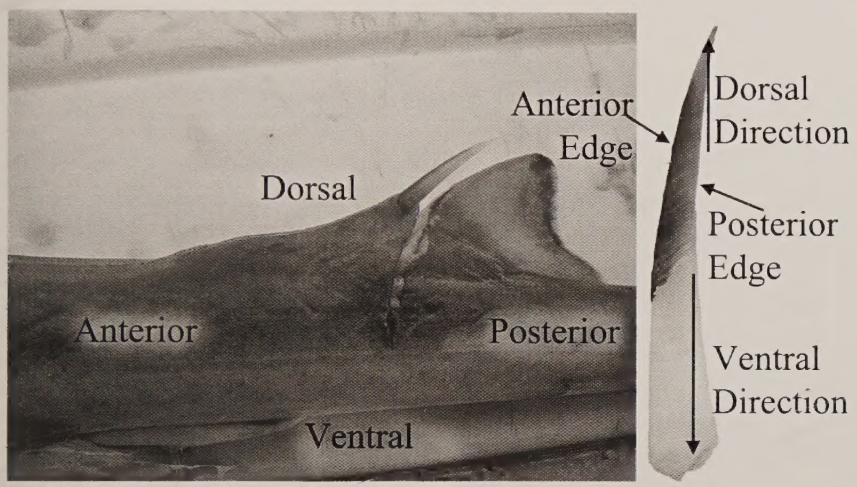

Figure 4.—Fin spine orientation.

and posterior edge (Fig. 5B). In general, a relatively larger LRD indicates a greater degree of wear.

If the LRP is improperly identified, over- or underestimation of the number of worn annuli can occur. For example, if the location of the annulus just ventral to the worn enamel is assumed to be the LRP, then the information in the area between that annulus and the worn edge of the enamel is lost, resulting in a potential overestimate of the number of worn annuli. Conversely, if annuli are evident dorsal to the worn edge of the enamel, as in both spines in Figure 5, it is inappropriate to identify the LRP dorsal to the worn edge of the enamel. This is because it is not possible to accurately measure the spine diameter at locations lacking enamel. Thus, measuring the diameter at this location would result in an underestimation of the true diameter at that point and a potential underestimation of the number of worn annuli.

Annuli are laid down as the spine grows in length. The oldest annuli are at the dorsal tip and those most recently formed are at the ventral edge of the enamel. The enamel gland deposits enamel as the spine grows from the base. In periods of slower growth annuli can be close together and sometimes appear to be stacked upon one another (Fig. 6). Growth patterns on the enamel do not appear to match those on dentine or the base cones (white structure) of the spine and the deposition mechanisms are different (Irvine et al., 2006). Thus, it is not possible to use the base cones or dentine to verify when annuli appear stacked on top of each other.

To estimate spine age, the dark bands are counted. For some spines, this is a relatively easy task (e.g., Fig. 5), but for others it can be much more challenging. In addition to being stacked upon each other (Fig. 6), annuli can appear compressed and almost indistinguishable in portions of the spine (Fig. 7). Annuli can also be very faint or diffuse, especially closer to the tip (Fig. 8A). For smaller animals, it appears that there are multiple "false annuli," or "checks," at the base of the spine. These fade with age and are less noticeable in older animals. This is likely caused by feeding pulses occurring in years of faster growth. While spiny dogfish are generalist feeders, they are also opportunistic and have been documented gorging when seasonal food sources are abundant (Tribuzio, 2010). For larger animals, the dark bands near the base are more distinct and are more likely to be true annuli. It is also possible to find spines with a bold white band at the enamel base (Fig. 8). This is the area where new annuli form but the enamel has not been laid down yet. If a dark area appears ventral to this white band, it is not counted in the age estimate.

There are a number of methods that have been used to make identifying annuli easier. Newer ventral portions of the enamel tend to have ridges associated with the dark bands (the older ridges, located more dorsally, are generally more worn), and dynamically adjusting the light source at different angles can be helpful in seeing the ridges. Only the most prominent ridges should be counted, as the smaller ridges between them are likely false

Figure 5.—A) Identification of the Last Readable Point (LRP) on worn fin spines from two different spiny dogfish. White arrows point to the LRP on the anterior edge of the enamel. The three small green arrows on the top fin spine highlight dark bands that should not be counted by the age reader because they are dorsal to the LRP. B) Side view, with white lines showing measurements of the fin spine diameter corresponding to the LRP.

annuli. A thin layer of mineral oil is also helpful to increase light reflection. When viewing the dorsal portion of the spine, where the enamel is thinner, shining reflected light on the spine from directly above can make it easier to see the color differences between dark bands while providing more contrast.

Additionally, spines can be viewed either dorsally or laterally to assist with identifying annuli and aid in following annuli around the spine. True annuli typically encircle the spine, whereas false annuli are often incomplete. Displaying spines on a monitor and either zooming out or standing back from the screen may aid in the identification of prominent dark bands. Applying color filters to high-resolution images of spines using image software such as Adobe Photoshop can also be helpful (Fig. 9). There are unlimited combinations of potential image transformations, and different transformations may be used for examining different portions of the spine. Transmitted light or polarizing filters have also been found to be useful when examining small or embryonic spines.

Interpretation of annuli can vary substantially between readers. To address this imprecision, a reference set of photographs of known-age specimens has been assembled, the ages of which were validated using bomb-radiocarbon dating (Campana et al., 2006). These specimens range in difficulty of interpretation from "easy" (Fig. 8A), where annuli are consistently spaced and relatively easy to identify, to "hard" (Fig. 8B), where annuli are more closely spaced and difficult to discern from one another on certain locations of the spine. These high resolution images and a set of calibration spines, for which multiple readers have come to an agreed age, are stored as part of the permanent collection of the NMFS Alaska Fisheries Science Center's Age and Growth Program and are available for future calibrations between readers and laboratories. Such reference sets are invaluable for evaluating accuracy of age estimates and

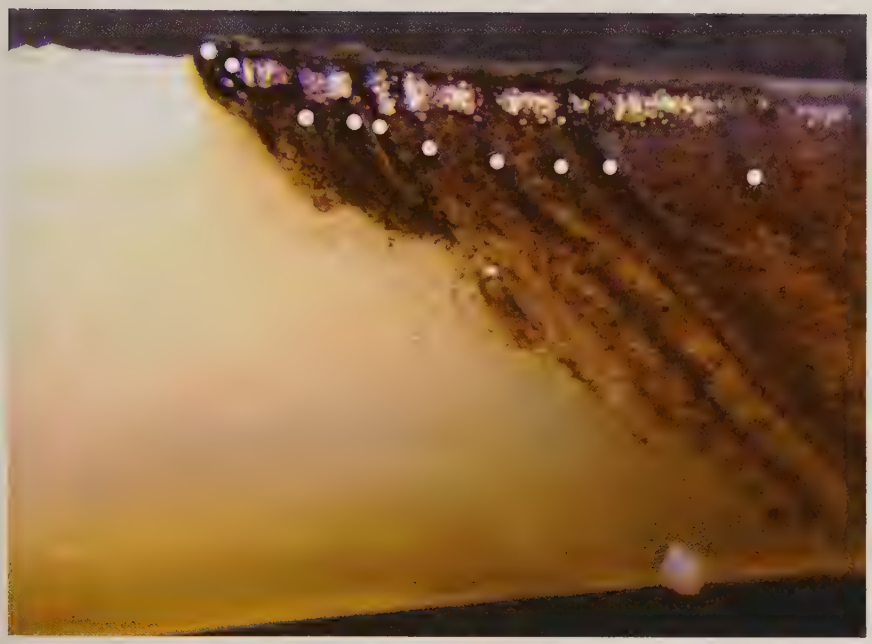

Figure 6.—Magnified image of spine enamel showing annuli stacked on top of one another. White dots identify ridges corresponding to annuli.

periodically testing inter-reader and inter-laboratory precision.

Vertebrae

Stained spiny dogfish vertebra thin sections are typically viewed with transmitted light, and fish age is estimated by counting the dark purple bands (Fig. 10). As with viewing spines, a number of filters either attached to the microscope or applied in imaging software can enhance contrast between light and dark bands. The morphological features of sectioned vertebrae are shown in Figure 11. Annuli are most easily seen on the corpus calcareum and radiate outwards from the focus. In many shark species, annuli can be followed through the intermedialia to the other edge of the corpus calcareum, but the intermedialia are absent or inconsistent in the *Squalus* species examined to date.

Vertebra measurements, if desired, should be taken along a single transect. The vertebra radius is taken from the focus (center) to the distal (outer) edge of the vertebra along the corpus calcareum (Fig. 11). Measurements are important for determining periodicity (i.e., marginal increment analysis), confirming location of the birthmark, and correlations between growth and annulus deposition.

Vertebrae accrete material around the focus as the shark grows. The annuli located closest to the focus are the earliest deposited, while those located furthest are the most recently deposited (Fig. 12). The growth pattern of an individual changes as it gets older, with the annuli closer to the focus being broader and more diffuse than the more distal (outer) annuli, which are thinner with sharper edges. The distance between annuli also decreases with increasing distance from the focus, such that annuli can become quite compressed in appearance near the distal edge of the vertebra (Fig. 12).

To determine age, first the location of the birthmark (age-0) must be identified. The birthmark usually corresponds with an angle change at the interface of the corpus calcareum and intermedialia (Goldman, 2004) (Fig. 12). The birthmark is excluded from the annulus count, and the following dark band is the first one counted in the age estimate. The birthmark's location may be confirmed by measuring vertebra radii of full-term embryos obtained from gravid females and comparing the average to measurements from the focus to the presumed birthmark on adult specimens.

Interpreting annuli on vertebrae, as with spines, is essentially counting the number of dark bands deposited. In some cases, determining what constitutes an annulus can be challenging,

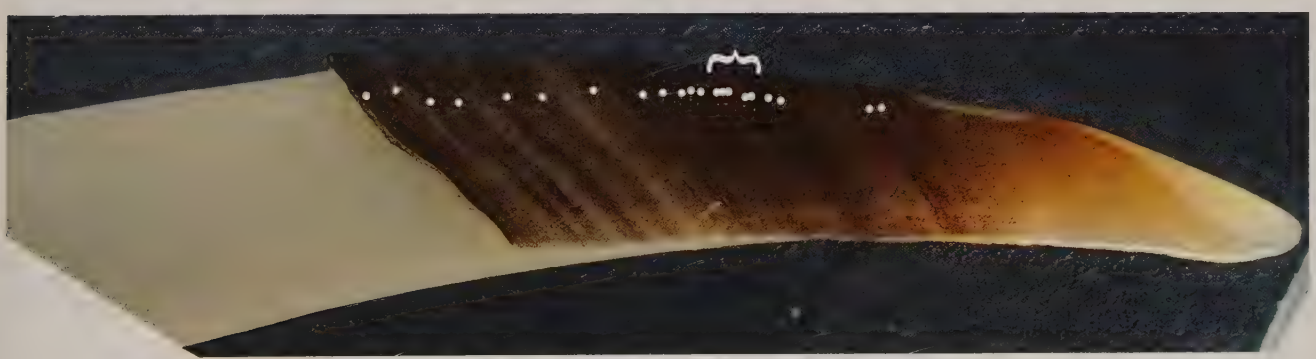

Figure 7.—Spine showing area with annuli very closely spaced or compressed. White dots identify selected individual annuli.

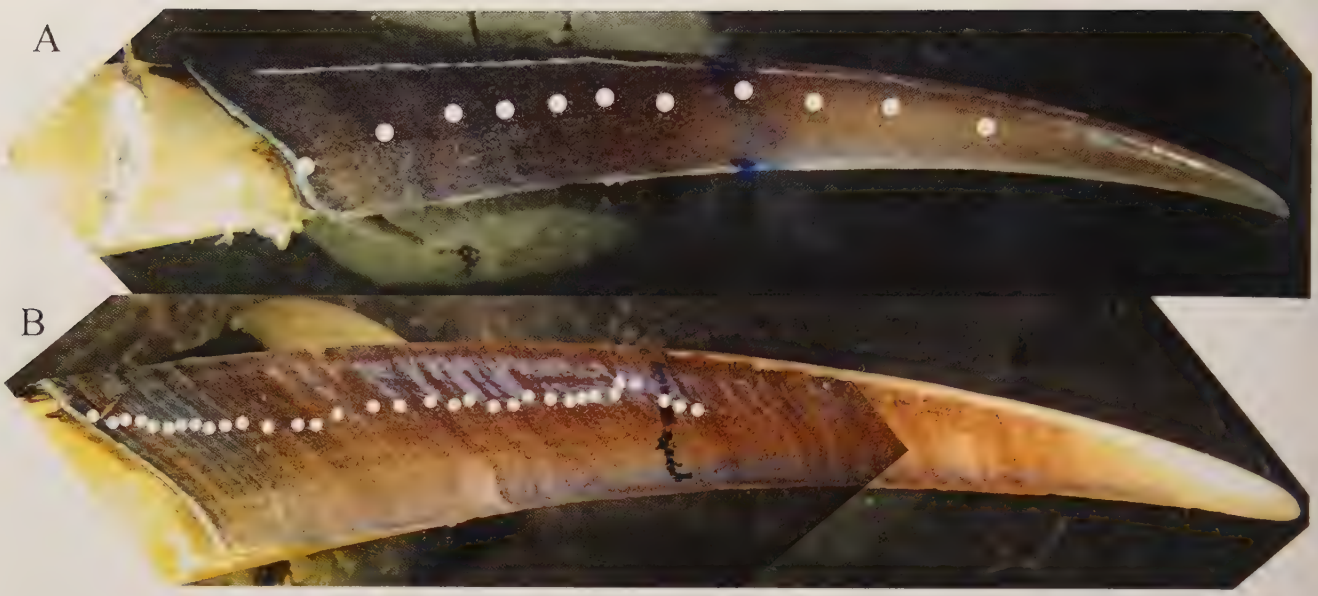

Figure 8.—Fin spines that are A) easy and B) difficult to interpret, with ages validated by bomb radiocarbon dating. Dots represent annuli. Images courtesy of the Canadian Shark Research Laboratory, Bedford Institute of Oceanography, Nova Scotia, Canada.

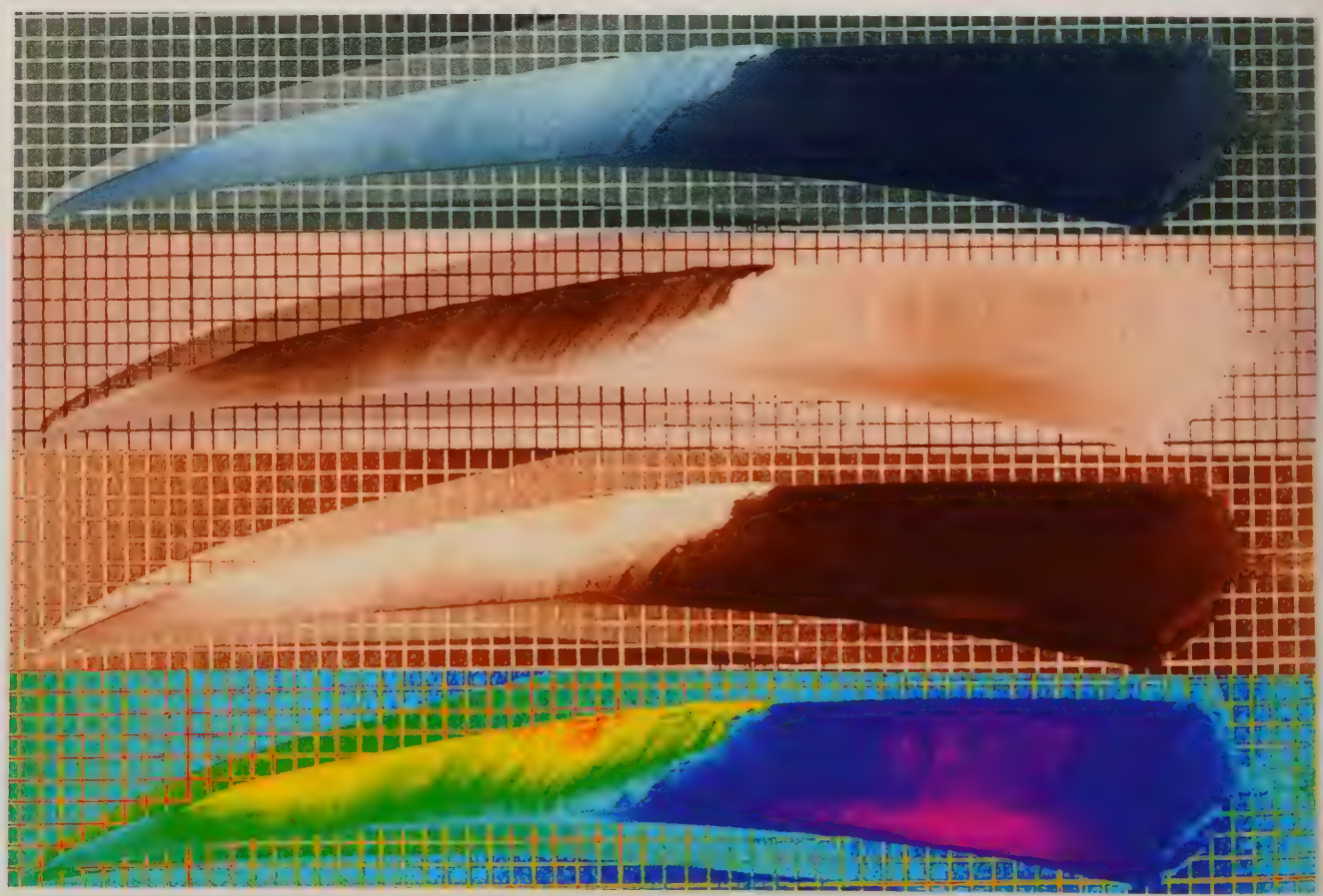

Figure 9.—Image analysis. Examples of four possible image transformations (performed using Adobe Photoshop Elements). From the top: inverted color, inverted then copper gradient, copper gradient only, rainbow gradient. Backgrounds are 1 mm x 1 mm grids.

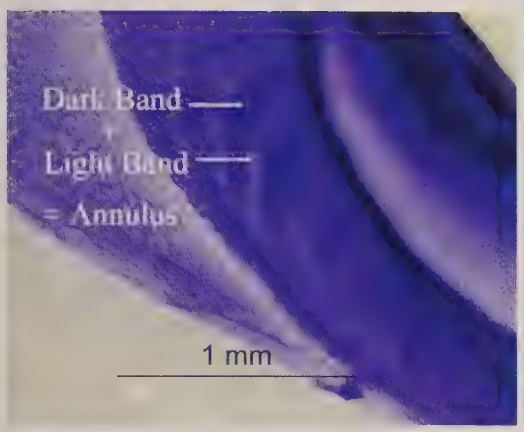

Figure 10.—Identifying bands and annuli on vertebrae.

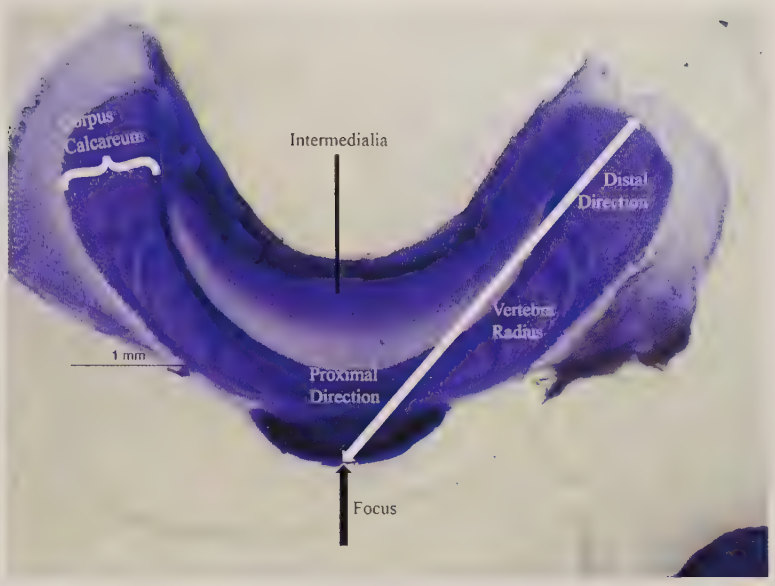

Figure 11.—Vertebra anatomy, with orientation and vertebra radius measurement shown.

Figure 12.—Sectioned and stained vertebra. Each dark band is marked with a white dot. The birthmarks are noted with red arrows. Note that annuli become more compressed with increased distance from the focus.

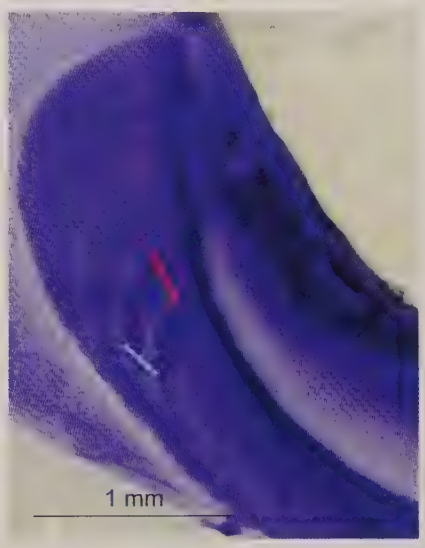

Figure 13.—Annulus width on vertebra (indicated by colored lines). Note the change in distance between annuli from the edge of the corpus calcareum nearest (red arrow) and furthest from the intermedialia (blue arrow).

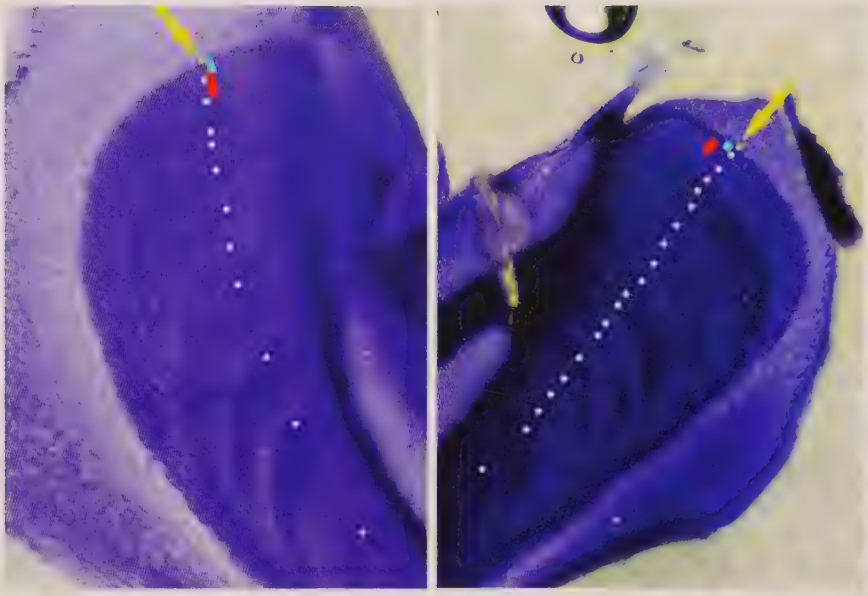

Figure 14.—Two different vertebrae with dark bands and marginal increment ratio (MIR) measurements identified. The blue line represents the edge width (EW) and the red line represents the last annulus width (LAW). The yellow arrow and dot mark the edge of the centrum.

while others are relatively easy to differentiate. By examining vertebrae using some of the following techniques, the reader can have more reproducible age estimates. If time allows, examining more than one vertebra per animal may also aid in age estimation.

Several criteria can assist with annulus identification. Annuli tend to be clearer and less compressed near the inner edge of the corpus calcareum (adjacent to the intermedialia) than on the outer edge (Fig. 13). However, the outer edges of the corpus calcareum can occasionally provide more evidence as there can be a slight notch corresponding to each dark band at the outer edge.

One must take into account the location on the vertebra in relation to the focus when determining whether a dark band is a single diffuse annulus or actually consists of multiple annuli, remembering that broad, diffuse annuli tend to be located nearest the focus. With increasing distance from the focus, annuli tend to become more condensed, requiring higher magnification. However, the vertebra may look somewhat granulated under higher magnification. It is sometimes easier to distinguish annuli near the focus by reducing magnification when viewing that portion of the vertebra.

The vertebra technique is relatively new for spiny dogfish and must be verified (or validated). Unlike spines, known-age vertebra samples are unavailable. The marginal increment ratio (MIR) is one method that is easily implemented and can be used to verify the annual periodicity of growth patterns. To compute the MIR, the reader measures the edge width (EW) and the width of the last fully formed annulus (LAW) (Fig. 14). The ratio of EW (blue line in Fig. 14) to LAW (red line in Fig. 14) is then averaged by month of collection to determine if the pattern of deposition is annual.

Similar to spines, a set of specimens aged by multiple laboratories and for which a consensus age was reached have been archived in a calibration collection, stored as part of the permanent collection of the NMFS Alaska Fisheries Science Center's Age and Growth Program.

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The Origins and Rise of Shark Biology in the 20th Century

JOSÉ I. CASTRO

Introduction

Historically, the knowledge of sharks (Elasmobranchii) has always lagged far behind the knowledge of bony fishes and other vertebrates. Several factors made sharks difficult to study. First, they are fast moving and far-ranging fishes in a vast marine environment, and the technology for studying such free-roaming aquatic animals did not exist. Second, it was difficult to obtain study specimens, owing to the historical lack of shark fisheries caused by their low commercial value. Third, the often large size of sharks made it difficult to preserve museum or reference specimens. Fourth, ichthyologists had a general lack of scientific interest in cartilaginous fishes, and few people studied sharks. Consequently, sharks long remained a poorly known group. This paper examines the origins of shark biology and the factors that combined in the second half of the twentieth century to 1) spark interest in sharks, 2) make shark research feasible, and 3) engender shark biology and conservation.

In general, comprehensive biological studies of animal species require both the anatomical examination of sufficient numbers of specimens to understand their adaptations and field studies to reveal the animal's behavior and habits. Over the centuries, most knowledge of animals was obtained through anatomical examination. Field observations of animal behavior were difficult or seldom feasible.

In the case of sharks, biological information could only be obtained through anatomical examination (necropsies) and from the analysis of limited capture or fishery data. In necropsies, stomach contents revealed the diet, and sometimes, by inference, behavioral or feeding patterns; examination of the reproductive tracts could reveal the mode of reproduction, reproductive cycle, gestation period, etc.

Observation and the application of the dictum of "Form follows function" often yielded an understanding of the animal. Analysis of capture data yielded depth and temperature preferences, migrations, nursery areas, etc. But because of the lack of fisheries, these data were scarce, so the biology of sharks remained a mystery.

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ABSTRACT—*Historically, the knowledge of sharks (Elasmobranchii) has always lagged far behind the knowledge of bony fishes and other vertebrates. In the 1950's, only a handful of researchers were working with or studying sharks. But, in the second half of the 20th century, four factors combined to spark interest in sharks, make shark research feasible, and engender shark biology and conservation.*

Those factors were 1) Generous funding of research on shark attacks and the use of sharks for military purposes by the U.S. Navy's Office of Naval Research; 2) A rise in popularity of recreational shark fishing and the development of marking tags that could be used to identify individual sharks; 3) The opening of China to commerce with the United States, resulting in a new shark fishery in U.S. waters and active shark fin markets. In turn, the rapid growth of the shark fin fishery and the geometric increase in the landings resulted in conservation concerns, and the eventual need for fishery regulations; and 4) The release of the movie "Jaws" engendered a fear of sharks and started a shark killing craze that became an ecological disaster.

"Jaws" affected the behavior and attitudes of millions of people toward sharks and the ocean, and the effects lasted for several decades. The effects of the movie were so deep, varied, and long-lasting that they eventually encompassed totally opposite behaviors.

The most significant impact of the movie "Jaws" was caused by the character "Matt Hooper." This character, and its personification, would have a profound and long-lasting effect on the young audience, for it told them that there was such a profession as "shark biologist" and that one could have a career studying sharks.

Youngsters who saw the film often fantasized about being shark biologists. Unfortunately, the sad reality was that there were very few positions available in shark research. A common trait and peculiar aspect of many young people, who were influenced by the movie and wished to become shark biologists, was their general lack of interest in biology or natural history. This was surprising, because curiosity about animals or their natural history has always been the sine qua non of biologists.

In a decade or two (~1995–2010), an unusual transformation occurred in the perception of sharks. In American society, sharks went from being feared animals to protected and even "totemic" animals. Totemism is a complex social phenomenon where individuals or groups form a mystical or emotional relationship with a venerated or sacred object, the totem, usually an animal. When sharks ceased to be fishes and became totemic animals, much of shark biology evolved into advocacy. Most of the logistical difficulties of the past are still with us, and shark research continues to be difficult. Today, much research is mainly concentrated on a few species of sharks, such as the totemic white shark, Carcharodon carcharias, *and the "charismatic" whale shark,* Rhincodon typus.

From the 18th century, the time of Linnaeus, to the 20th century, shark studies were limited to descriptions of the animals or their anatomy. In the early 20th century, Sheldon (1909, 1911) and Parker (1910, 1914) carried out the first sensory laboratory experiments on sharks, using smooth dogfish, *Mustelus canis*. Despite these early experiments, throughout the first half of the 20th century, shark research was usually limited to taxonomic studies; only a few biological studies were carried out (Gudger, 1907, 1949; Gudger and Smith, 1933). Thus, there was little progress in the understanding of sharks.

In the late 1930's and early 1940's, shark fisheries developed in North America as uses for shark leather and liver oil were discovered. Extensive and intensive fisheries developed for the soupfin shark, *Galeorhinus galeus* = *zyopterus*, ranging from California to Washington (Byers, 1940; Ripley, 1946; Westrheim, 1950). On the U.S. east coast, a more extensive fishery developed primarily for the sandbar shark, *Carcharhinus plumbeus*, although the fishery was not as intensive as the west coast fisheries.

These fisheries could have engendered studies on sharks, but at that time few biologists were interested in sharks. Thus, despite the large numbers of sharks taken in the fisheries, only one species, the soupfin shark, was studied. Detailed studies were carried out on the soupfin shark and its fishery (e.g., Ripley, 1946; Bolomey and Sycheff, 1946), although most of the studies were industrial rather than biological.

On the east coast, no agency collected data on the sharks or the fishery. The only person who examined large numbers of sharks at that time was Stewart Springer, who had started as a fisherman for Shark Industries, Inc.[1], and later became a biologist for the U.S. Bureau of Commercial Fisheries (BCF) (Castro, 2013). Springer published what little data existed on the fishery (Springer, 1952). Later he published his monograph on the sandbar shark (Springer, 1960), based on records obtained while employed by the Shark Industries Division of the Borden Company (in the 1940's and early 1950's) and later while conducting exploratory fishing aboard BCF R/V *Oregon*.

In 1937, the Sears Foundation for Marine Research was established at Yale University. One of the Foundation's first projects was a series of scholarly books titled "Fishes of the Western North Atlantic." The first volume of the series, published in 1948, covered lancelets, cyclostomes, and sharks. The shark section was written by Henry B. Bigelow and William C. Schroeder of the Museum of Comparative Zoology at Harvard University.

This publication (Bigelow and Schroeder, 1948), was basically a taxonomic work but also summarized what little was known then about the biology of sharks of the western North Atlantic. The book remained the standard reference on sharks for several decades, and it set such a high standard for the series that subsequent volumes came out at a very slow pace.

The Dawn of Shark Biology

By the 1950's, the shark fisheries were a thing of the past. There were virtually no shark fisheries in North America, and anyone wanting to study or conduct research on sharks had to acquire his or her own specimens. Thus, biological studies of sharks were extremely difficult to carry out and people who studied sharks were rarae aves.

In late 1954, Alfred C. Vanderbilt and Eugenie Clark founded the Cape Haze Marine Laboratory in Placida, Fla. Soon after the laboratory opened, Clark began catching sharks at the request of a fellow scientist, John H. Heller, who had gone to the Caribbean to collect sharks for research and had failed to obtain them. Soon, Clark was the only scientist regularly catching sharks, keeping them in captivity in pens open to the sea, and conducting behavioral experiments on them (Clark, 1959).

Clark and her fishermen set longlines periodically for sharks. Large specimens that were alive on the lines were transferred to the sea pens for experiments; dead sharks were necropsied, and Clark took extensive notes on their anatomy and condition.[2] These studies eventually produced Clark's first reports on learning in sharks (Clark 1962, 1963), and one of the few comprehensive biological studies of the sharks of central Florida (Clark and von Schmidt, 1965). Few other biological studies of sharks were produced at the time because specimens were difficult to obtain because the lack of fisheries.

In the mid-1950's, the main interest on sharks was in developing repellents (Castro, 2013). Recent experiences from World War II in the tropical Pacific Ocean had demonstrated that downed naval aviators and sailors and mariners whose ships had sunk were highly vulnerable to shark attacks (Llano, 1955, 1963). In April of 1958, a conference titled "Basic Research Approaches to the Development of Shark Repellents" was held in New Orleans, sponsored by the American Institute of Biological Sciences (AIBS) and Tulane University, and funded by the Office of Naval Research (ONR) and the Bureau of Aeronautics. A total of 34 participants from across the world attended the conference. The conference proceedings were later compiled into the book "Sharks and Survival" (Gilbert, 1963a). The book is mainly about shark attacks (12 of its 22 chapters), and only 10 chapters can be said to deal with shark biology.

Authors of the biological chapters were Conrad Limbaugh, Stewart Springer, Eugenie Clark, Albert L. Tester, Lester Aronson, Richard Backus, and Perry W. Gilbert. Conrad Limbaugh was a Marine Diving Specialist from Scripps Institution of Oceanography who perished in a 1960 cave diving accident in France. Lester Aronson

[1]Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service/NOAA.

[2]Clark's notebooks, with extensive notes on each specimen examined, remain at Mote Marine Laboratory, Sarasota, Fla., and the author used them extensively while writing "The Sharks of North America" (Castro, 2011).

Erasmus Darwin and Sharks

The idea of controlling and harnessing sharks predates the attempts of the Office of Naval Research by nearly 200 years. Erasmus Darwin (1731–1802), was an English physician, botanist, natural philosopher, inventor, abolitionist, and poet; an extraordinary man and one of the influential thinkers of the English Enlightenment. Erasmus Darwin was a founder of three scientific societies, including the famous Lunar Society of Birmingham, a discussion group of experimentalists, inventors, and savants of the age who met during the period of the full moon in the 1770's–1790's (they met during the full moon to facilitate the members' travel home in the days before street lighting).

Darwin was also a prescient and far-sighted individual who foresaw the automobile, the steamboat, the submarine, and the aircraft. A prototype steam vehicle existed in France by 1769, and in 1781, James Watt patented a steam engine that produced continuous motion. Darwin foresaw that steam could soon be applied to many devices: In *Canto X* of The *Botanic Garden*, Darwin (1791) wrote:

"Soon shall thy arm, unconquered Steam! afar
Drag the slow barge, or drive the rapid car;
Or on wide-waving wings expanded bear
The flying-chariot through the fields of air.
Fair crews triumphant, leaning from above,
Shall wave their fluttering kerchiefs as they move;
Or warrior-bands alarm the gaping crowd,
And armies shrink beneath the shadowy cloud.

Erasmus Darwin also conceived the submarine, solving the problem of respiration inside the submarine by means of oxygen gas which had been discovered (as "dephlogisticated air") by his friend Joseph Priestley a decade earlier, and recently (1789) explained by the French chemist Antoine Lavoisier* (McKie, 1952). Knowing that the steam engine could not operate underwater, and the effective internal combustion engine still about a century away, he needed a mode of propulsion for his underwater craft (Slosson, 1923). Then he conceived the idea of harnessing sharks in the manner of horses:

Led by the Sage, lo! Britain's sons shall guide
Huge *Sea-Balloons* beneath the tossing tide;
The diving castles, roof'd with spheric glass,
Ribb'd with strong oak, and barr'd with bolts of brass,
Buoy'd with pure air shall endless tracks pursue,
And Priestley's hand the vital flood renew.--
Then shall Britannia rule the wealthy realms,
Which Ocean's wide insatiate wave o'erwhelms;
Confine in netted bowers his scaly flocks,
Part his blue plains, and people all his rocks.
Deep, in warm waves beneath the Line that roll,
Beneath the shadowy ice-isles of the Pole,
Onward, through bright meandering vales, afar,
Obedient Sharks shall trail her sceptred car,
With harness'd necks the pearly flood disturb,
Stretch the silk rein, and champ the silver curb;
Pleased round her triumph wondering Tritons play,
And Seamaids hail her on the watery way.

In his *Zoonomia* (1794), a two volume rambling work attempting to classify facts about animals and to set out laws of organic life, Erasmus Darwin anticipated evolution by natural selection: "since the earth began to exist...would it be too bold to imagine, that all warm-blooded animals have arisen from one living filament... possessing the faculty of continuing to improve by its own inherent activity, and of delivering down those improvements by generation to its posterity." Over 50 years later, in 1859, his grandson, Charles, who read it and commented on "Zoonomia," would publish his own theory of evolution by natural selection (Darwin, 1859). For interesting biographies of Erasmus Darwin see Darwin (2002), and King-Hele (1963).

*Joseph Priestley was a member of that group. He is credited with the discovery of the component of air that was needed for respiration and life. He called it 'dephlogisticated air," and we now call it oxygen. In 1789, the French chemist Antoine Lavoisier named the gas oxygen and explained that water consisted of hydrogen and oxygen. Erasmus Darwin was evidently aware of these discoveries.

was an anatomist and behaviorist at the American Museum of Natural History (and one of Eugenie Clark's mentors). His contribution to the symposium was a descriptive article on the central nervous system of sharks and bony fishes. Most of his previous works were on poeciliid fishes and domestic cats, *Felis catus*, and he cannot be said to have been a shark specialist. Stewart Springer was a great naturalist and a shark fisherman of considerable experience. He was an autodidact who learned much by butchering and dissecting thousands of sharks. The other four (Clark, Gilbert, Tester, and Backus) were just beginning their shark researches. So, at that time, only a few people in the United States could be listed as researchers of shark biology.

Then, in June 1958, the AIBS Shark Research Panel was established to "1) expedite and activate recommendations formulated at the ONR sponsored conference on Basic Research Approaches to the Development of Shark Repellents and 2) to serve as clearing house for all information related to the field of elasmobranch biology in general and to the shark hazard problem in particular" (Olive, 1971). This panel was chaired by Perry W. Gilbert (Cornell University) and included Sid-

ney R. Galler (ONR), John R. Olive (AIBS), Leonard P. Schultz (USNM), and Stewart Springer (BCF). In subsequent years, Albert L. Tester (University of Hawaii), and H. David Baldridge (USN) were added to the panel. From 1958 to 1970, the panel initiated basic research on sharks, funded research on anti-shark measures or repellents, organized conferences, and maintained the Shark Attack File, a data collection system based on five newspaper clipping services which gathered information on shark attacks worldwide.

From the early 1960's to the mid-1970's, four factors would converge to change the feasibility of shark research. First, generous funding of research on shark attacks and the use of sharks for military purposes by the Office of Naval Research (Castro, 2013) allowed some researchers to keep sharks in captivity and to carry out sensory and physiological experiments on them.

Second, a rise in popularity of recreational shark fishing and the development of marking tags that could be used to identify individual sharks, resulted in popular shark tagging programs that marked thousands of sharks. These efforts produced research specimens and significantly increased the knowledge of sharks and their migrations.

Third, the opening of China to commerce with the United States resulted in the development of a new shark fishery in U.S. waters and active shark-fin markets, producing abundant research specimens. The rapid growth of the shark fin fishery and the geometric increase in the landings also resulted in conservation concerns and the eventual need for fishery regulations to protect the shark stocks. Because fishery management required knowledge of shark species, populations, and landings, this knowledge had to be acquired promptly.

Fourth, the release of the movie "Jaws" in 1975 had significant effects that have lasted for decades: It engendered a fear of sharks and started a shark killing craze that lasted two decades. Shark fishing tournaments proliferated and became an excellent source of specimens for researchers. Additionally, the movie images of the shark biologist would influence a generation of young viewers to seek careers as shark biologists.

The First Factor: ONR, Sharks, and the Military

When World War II ended in 1945, a new world order ensued, with two superpowers of totally different ideologies, the United States and the Soviet Union, struggling for supremacy. For the next decades, the superpowers prepared for the possible next war by developing new weapons (intercontinental ballistic missiles, nuclear submarines, super-aircraft carriers, etc.) while engaging in the confrontations and proxy wars that became known as the Cold War.

In January 1954, the first nuclear-powered submarine, the USS *Nautilus*, was launched. It was a revolutionary new ship that shattered all existing records of submerged speed and endurance. Some 50 years earlier, the British had launched HMS *Dreadnought*, a revolutionary battleship, the first fitted with turbines and larger guns, which made obsolete all previously built battleships.

The *Dreadnought* started a "battleship race," in which, for the next four decades, nations continually endeavored to build bigger, faster battleships with bigger guns than their potential enemies. The *Nautilus* started a similar race where the two superpowers built bigger, faster, and stealthier nuclear submarines armed with increasingly more powerful missiles and torpedoes. This race for better submarines, which has lasted to this day, required new concepts, new materials, and new technologies.

Based on my analysis of the research funded by the ONR, the National Aeronautics and Space Administration (NASA), and the Defense Advanced Research Projects Agency (DARPA), beginning in the 1960's, it appears that the managers expected that much could be learned from the adaptations of sharks. It was recognized that these creatures were the product of millions of years of evolution towards efficient, effective, and stealthy marine predators, and those adaptations perhaps included principles of drag reduction, prey sensing, stealth, etc. that could be applied to military equipment.

Thus, these agencies funded research on shark vision (Gilbert, 1963b), chemoreception (Hodgson and Mathewson, 1978), electric and magnetic senses (Kalmijn, 1978), hydrodynamic aspects of shark scales (Raschi and Musick[3]), and many other projects (and not just in sharks) in search of principles or ideas that could be applied to submarines or other new weapons. The ONR continued to fund shark research for many years and most of the knowledge of sharks acquired in the second half of the twentieth century was based, or at least partially based, on research funded by ONR.

The effects of such funding on shark research cannot be overestimated; ONR funding created and greatly advanced shark biology. The research was generally geared to discovering how sharks were such effective predators, hoping to make submarines more shark-like, but in the late 1960's, research took a new direction: sharks as weapon deliverers.

Sharks as Weapon Carriers: An Analysis

It is likely that no one noticed when in 1967–68, the U.S. Navy assigned two top scientists, Clarence Scott Johnson and Henry David Baldridge, to the then little-known, financially strapped Cape Haze Marine Laboratory in rural central Florida[4]. Johnson had a Ph.D. in Nuclear Physics and was a physicist at the Naval Undersea Warfare Center, San Diego, with a background in the training of marine mammals for military purposes.

[3]Raschi, W. G., and J. A. Musick. 1986. Hydrodynamic aspects of shark scales. NASA Contr. Rep. 3963, Prep. for Langley Res. Cent. under Contr. NAS1-16042, NASA CR-3963 19860013418. Sci. Tech. Info. Br., NASA.

[4]The name of the laboratory was soon changed to Mote Marine Laboratory. ONR funding allowed the laboratory to survive.

Baldridge was a naval captain with a Ph.D. in Organic and Physical Chemistry from the University of California at Berkeley. Why would the U.S. Navy assign such capable and valuable researchers to a sleepy marine laboratory in rural Florida? According to Gerald D. Sturges (1982), these scientists came to Florida to work on "Project Headgear," to "convert the shark into a remote-controlled torpedo that could ram a ship while carrying a load of explosives."

The idea of using animals to deliver explosive or incendiary materials to the enemy was not new. During the early stages of World War II, the Nazi and Japanese juggernauts could not be stopped by the Allied Nations, which had long neglected their armed forces. In those bleak and desperate years, the Allies hatched many schemes to replace the war materiel they lacked with animals as weapons. Thus, the Allies created mine dogs, bat bombs, and exploding dead rats.

The Soviets invented the "mine dogs," anti-tank dogs carrying a mine with a contact detonator strapped to their back. These dogs were trained, often by starvation, to feed under Soviet tanks. The idea was that later they would approach the formidable German Panzer tanks and crawl under them causing the mine to blow up tank and dog.

According to Generaloberst Erhard Rauss (1995), who commanded the 3rd and 4th Panzer Armies in Russia, there is no evidence of any German tank destroyed by a mine dog. On the contrary, it was reported that mine dogs, frightened by the firing and noise coming from the German tanks, fled and sought protection under the Soviet tanks, which promptly blew up, or they ran back to their handlers, with similar results. Rauss (1995:76) concluded that "One thing is certain: the specter of mine dogs ceased just as abruptly as it had begun."

In the United States, a similar idea to the mine dogs was hatched in 1942: to strap small incendiary devices to bats and then release the bats from aircraft over Japan. The bats would then fly down and roost in highly-flammable wooden Japanese structures, causing conflagrations. The "bat bomb" idea (Project X-Ray) proved its feasibility on 15 May 1943 when a few torpid bats, outfitted with live incendiaries for a "photo session," became active and escaped with their deadly devices. Most of the escaped bats landed at the nearby and newly constructed Carlsbad Auxiliary Airfield. Fifteen minutes later, the bats incinerated the airstrip control tower, adjacent barracks, offices, and hangars (Couffer, 1992). The bats, however, were never used operationally. The B-29 Superfortresses, incendiary bombs, and General Curtis LeMay were sufficient to incinerate the Japanese cities.

Who conceived the idea of using sharks as weapons in Project Headgear is not known to the author. It is likely that those who conceived the project were influenced by the World War II precedents of the mine-dogs and the bat bomb, and by the training of marine mammals for naval use. After those precedents, the idea of a shark as a guided animal torpedo likely appeared logical and feasible. Perhaps sharks could achieve something technology could not do at that time. Project Headgear started in the days of the Cold War and the Space Race, and anything that could be used to gain an edge over the Soviets was probably deemed a reasonable effort or expenditure.

Much of the work was carried out in two circular tanks made for the project at Mote Marine Laboratory and at a second facility for shark research at the Lerner Marine Laboratory (Fig. 1), Bimini, Bahamas. The Lerner facility made it possible for the first time to "work experimentally with large elasmobranchs up to 15 feet in length" (Gilbert and Kritzler, 1960:424).

The details of sharks carrying weapons under "Project Headgear" have never been released. It appears that the project remains classified, almost 50 years later, because the author's requests to the Office of Naval Research, including requests under the Freedom of Information Act, have not produced any information. According to the ONR, "There are no responsive records."

However, an analysis of papers published by the Project Headgear researchers confirms Sturges' assertions, and indicates the nature of the problems the investigators encountered and attempted to solve. If sharks were to be used to carry a "payload," there were two problems that had to be solved. First, how do you guide a shark to its target? Second, how much weight can a shark carry? The problems of weapon design would be simple in comparison, and are irrelevant here.

It appears, based on the duration of the project, that the researchers worked on the guidance of sharks first, and initially ignored the second question of how much weight could be carried by a shark. Had they investigated the second question first, the project would have been deemed unfeasible and stopped.

How the movements of a shark could be controlled had been known for a long while. Parker (1910, 1914) demonstrated that a smooth dogfish with an occluded nostril would usually turn toward the side of the non-occluded nostril; that is, towards the side receiving a stimulus. The Parker experiments suggested that by impinging on the shark senses, the direction of the animal's movement could be controlled. Given the anatomy of the shark brain, it would be relatively easy to insert an electrode into the olfactory lobe or the long olfactory nerve, stimulating it and causing the shark to veer towards the stimulated side. Alternatively, other cranial nerves could probably be used with similar results.

Nevertheless, based on the papers written on buoyancy by Baldridge (1970, 1972), the load carrying ability of sharks was eventually investigated. If the researchers looked at the carrying capacity of bats in Project X-Ray or at data on bird flight, they were certainly misled on the potential of sharks as weapon carriers.

In 1943, bat bomb personnel had discovered that a Mexican freetailed bat, *Todarida brasiliensis*, weighing

Figure 1.—A. Early shark pens used for Project Headgear at the Lerner Marine Laboratory, Bahamas. B. Improved shark pens for the project. (From Lerner brochures).

10–11 g could carry a weight of 15–18 g, more than its own weight. Thus, a pyrogenic device was designed and constructed that was light enough to be carried by a bat. The bat bomb device, carried by the bats which incinerated Carlsbad Auxiliary Field, consisted of a celluloid case filled with napalm (jellied gasoline), along with its igniter, and weighed only 17.5 g.

Years later, Davis and Cockrum (1964), in tests also funded by ONR, obtained much reduced loads, about 9.3% of the bat weight for the Mexican free-tailed bat. But they also reported that other species of bats could carry up to 73% of their body weight. They stated that the discrepancy may be due in part to the bomb bats being released from considerable heights (and thus just flying downwards). In any case, bats, with their large wings, are great load carriers, but the size of the load is minute due to the small size of the bats. It is likely that the researchers reasoned that, if a little bat could carry such proportionally great loads, a big shark weighing several hundred pounds should certainly carry a heavy load.

However, to carry "a load of explosives," Project Headgear scientists had chosen the wrong type of animal, because sharks are poor load carriers. Let's explain! First, for mechanical purposes, sharks must be regarded as "flying" animals, not swimming animals. It may be best to briefly recall some basic physical principles. Flight is movement through a fluid, be it air or water, where a lift force is generated when an object moves through the fluid, and it is generally directed upward. Drag is a force caused by the fluid in the opposite direction to the movement of the object. Thrust is the force generated by wing or tail flapping and is in the direction of animal's movement.

Flight results from achieving the requisite combination of forces: thrust, lift, and drag, and overcoming gravity. Accumulating all the morphological changes and adaptations through evolution, and achieving the needed combinations that enabled animals to fly must have taken eons. Before an

animal could get off the ground or sea bottom, it had to evolve adaptations such as reduction of structural weight (e.g., with air sacs and hollow bones in birds, and lightweight cartilaginous skeletons and oil-filled livers that produce buoyancy in sharks) and reductions in drag (form streamlining, and surfaces that induce laminar flow, such as feathers in birds and skin denticles in sharks).

Flight is a wonderful evolutionary advantage, and, in nature, true flight is a rare adaptation. Most authors consider that true flight (powered or "flapping"), as distinguished from gliding, parachuting, and soaring, has evolved only three times in the long vertebrate histories: in reptiles (in the extinct flying reptiles or pterosaurs), birds, and bats (Romer, 1966; Norberg, 1990). Perhaps these authors should specify "aerial flight," because, for mechanical purposes, sharks fly through the water.

Sharks lack swim bladders, and thus, their specific gravity is greater than that of seawater. Therefore, sharks are incapable of floating like bony fishes.[5] Sharks must keep moving to obtain lift from their fins and body, lest they fall to the bottom, just like a bird or an airplane must keep moving or it falls from the sky. The mechanics of flight are the same for shark, bird, or airplane.

At some point the researchers had to answer the question of what load sharks could carry, and this was probably the fatal question that doomed the project. Evidence indicates that they investigated the load carrying capacity of sharks by measuring the buoyancy of sharks. Baldridge, a first-rate scientist with a brilliant mind, had no training in biology. However, within a couple of years of arriving in Florida, he produced the two classic papers on the specific gravity of sharks and on how the sharks achieve neutral buoyancy: "Sinking factors and average densities of Florida sharks as functions of liver buoyancy" (Baldridge, 1970), and "Accumulation and function of liver oil in Florida sharks" (Baldridge, 1972). Later, Baldridge (1982) wrote an article titled "Sharks don't swim, they fly" where he displays full understanding of the mechanics of swimming and lift in sharks, and demonstrates that he understood, back in the 1970's, that for mechanical purposes sharks fly through the water.

The Baldridge studies also demonstrated that, when compared to other flying animals, sharks are poor load carriers. Perhaps, the relative size of shark pectoral fins (Fig. 2), or their "wings," is much smaller than that of birds and bats, and shark fins do not provide enough lift for carrying extra weight (Lift varies directly with area of the wing, the density of the fluid, the square of the velocity, and angle of attack). There was no need for sharks to evolve load-carrying adaptations.[6] It is likely that, after his buoyancy tests, Baldridge saw the fatal flaw that his colleagues, or the originators of the project, had failed to understand at its inception.

The realization that a large shark could not carry a sufficiently large explosive probably doomed the project. Today, over 45 years later, Baldridge's papers remain the best source of knowledge and empirical data on buoyancy in sharks. Unfortunately, the other experiments carried out during the project have not been published and remain hidden from view.

Other Laboratory Studies

Despite the problems with Project Headgear, project personnel were quite productive and carried out other laboratory activities, probably as a cover for their real mission. Johnson developed the "Shark Screen," a large "imperforate bag formed of thermoplastic material" with inflatable compartments where a shipwrecked person could float and hide from sharks (U.S. Patent #3,428,978, dated 25 Feb. 1969). Johnson and Baldridge later cooperated on the "Electric Anti-shark Dart," a device mounted on a spear shaft, and used for incapacitating sharks and other marine predators (or diver?) by means of an electric current, without creating noise or bloodying the water which often would attract other predators (U.S. Patent #3,771,249, dated 13 Nov. 1973).

Baldridge "conducted research towards basic scientific approaches to the development and testing of both physical and chemical shark deterrents," and compiled and analyzed data on shark attacks throughout the world. Castro (2013) provided details of Baldridge's work on shark repellents. Johnson would later publish papers on cetacean communication and a charming little book on how to train goldfish, *Carasius auratus*, using dolphin, *Tursiops* spp., training techniques (Johnson, 1995).

The ideas of learning some of the secrets of the evolutionary success or predatory efficiency of sharks and of using sharks for military purposes have continued to fascinate the military research agencies for over six decades, and attempts at controlling sharks continue to this day. In recent years, DARPA funded researchers at the University of Michigan to develop "implantable neural interfaces in freely swimming sharks in order to investigate neural coding associated with sensory processing and natural behavior" (Kipke et al.[7]). A press correspondent translated this as "to direct the shark by directly controlling its senses," while a researcher spoke of it as "to direct a shark by remote control" (Cooke, 2004). Déjà vu.

[5]A few sharks, such as the sand tiger shark, *Carcharias taurus*, often seen in aquariums, appear stay almost motionless. Sand tiger sharks are known to gulp air, which must enhance their buoyancy. It has been suggested that sleeper sharks, *Somniosus* spp., might be able to stay almost motionless by seal breathing holes, in wait of their prey. This has yet to be demonstrated.

[6]Unlike birds, sharks evolved viviparity. Thus, females of viviparous sharks are burdened by having to carry to term a brood of large young. How female sharks compensate for this load is unknown.

[7]Kipke, D. R., J. Carrier, and D. J. Anderson. 2007. Implantable neural interfaces for sharks. Final Tech. Rep., Contr. HR0011-05-C-0018, dated 31 May 2007. Defense Advanced Res. Proj. Agency (DARPA), Arlington, Va.

The Second Factor: Tags and the Tagging Era

Early Shark Tags

During 1936–48, Hansen (1963) applied brass tags, known as Petersen discs, to the jaw and pectoral fins of Greenland sharks, *Somniosus microcephalus*, to study their growth and migrations in the Arctic. This appears to be the first use of tags to study sharks, although bony fishes had been marked or tagged for many years (McFarlane et al., 1990).

The tagging of sharks for research purposes did not begin in the United States until nearly three decades later. In 1961, the Department of Interior's Bureau of Sport Fisheries and Wildlife established the Sandy Hook Marine Laboratory, the first federal laboratory in the United States specifically dedicated to study the migratory marine game fishes (Casey, 1985).

In 1960, two shark attacks on swimmers off New York and New Jersey (McCormick et al., 1963), had raised the question of what species of sharks inhabited the area and what level of hazard they represented. This generated support for shark studies at the Sandy Hook Laboratory in 1961. The research vessel *Cape May* was loaned to the laboratory by the Smith Research and Development Corporation of Lewes, Del., for the purpose of a longline survey of sharks between Long Island and Delaware Bay from late August to early October 1961 (Casey, 1985). Over 300 sharks were caught in the survey, including white sharks, *Carcharodon carcharias*; tiger sharks, *Galeocerdo cuvier;* dusky sharks, *Carcharhinus obscurus*, and other large species which were considered potentially dangerous to swimmers (Casey, 1985).

Release of the survey results stimulated a great interest in sport fishing for sharks, rather than an increase in apprehension over shark attacks. Hundreds of fishermen wrote to the Sandy Hook Laboratory requesting information on shark fishing. Subsequently, a recreational shark fishery developed off the northeastern United States,

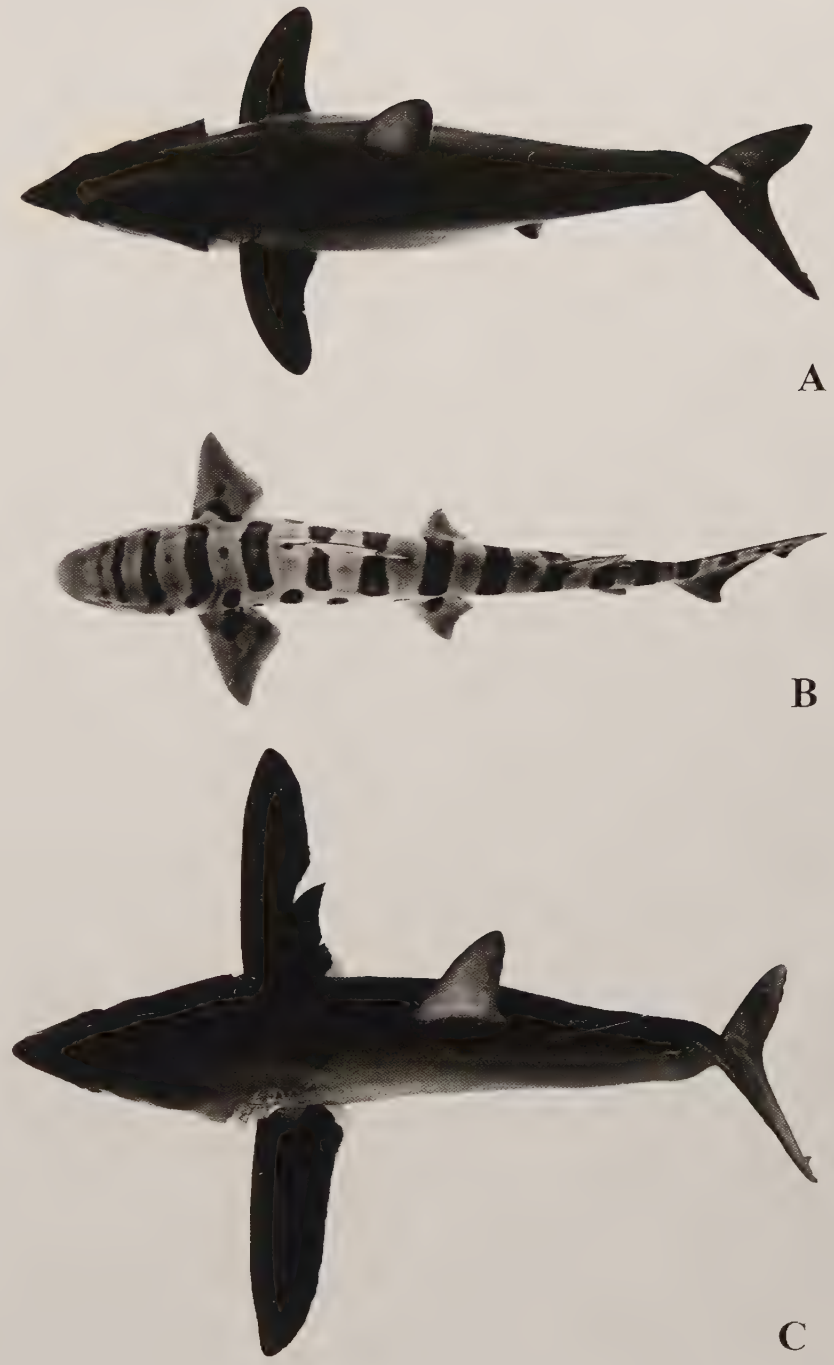

Figure 2.—Dorsal views of different sharks showing the small pectoral fins. A. Shortfin mako, *Isurus oxyrinchus*, B. Leopard shark, *Triakis semifasciata.* C. Longfin mako, *Isurus paucus.*

and expanded along the entire Atlantic coast (Casey, 1985).

In 1962, the growth of the recreational shark fishery made it possible for John G. Casey of the Sandy Hook Laboratory to develop a volunteer-based Cooperative Shark Tagging Program (CSTP) to understand the migrations of sharks (Casey, 1985; Kohler et al., 1998). In 1966, the NMFS tagging studies were transferred to the Narragansett Laboratory, where Casey continued to expand his volunteer program.

Two basic types of tags were used in the early tagging program: a fin tag (known as the Jumbo Rototag), and a dart type (the "M" tag). The M tag had been developed by Frank Mather, III, for use with tunas (Scombridae), and modified by Casey for use in sharks. These tags yielded information only when a tagged fish was recaptured at a later date. Knowing the tagging and recapture locations, the general direction of the animal's movements could be determined. Much later, in the next century, these tags would be referred to in retrospect as the "dumb tags" when compared to the "satellite archival tags" which yielded more extensive tracks of the sharks' movements.

Despite the primitive tags, the CSTP was eminently successful. Between 1962 and 1993, some 6,500 volunteers tagged 106,449 sharks of 33 species. The information obtained through the tagging program allowed biologists to start to understand the complex habits and migrations of sharks. The program also generated a great deal of enthusiasm among sport fishermen for tagging and releasing sharks. The results of this long-term, broad-scale effort were published in a tagging atlas summarizing the migrations of sharks off the eastern United States (Kohler et al., 1998).

The Rise of the Modern Tags

Toward the middle of the twentieth century, a few zoologists armed with binoculars and great patience learned to approach and observe large, free roaming terrestrial animals in their natural habitat. Even large primates such as gorillas, *Gorilla gorilla*, and chimpanzees, *Pan troglodytes*, were studied by Schaller (1963) and Goodall (1986), respectively. However, the observational techniques used at that time could not be applied to all animals or all habitats.

Some very secretive jungle-dwelling animals such as tigers, *Panthera tigris*, and jaguars, *Panthera onca*, or wide-ranging animals such as wolves, *Canis lupus*, and moose, *Alces alces*, were almost impossible to track and observe. Free ranging marine animals were "out of the question" in that era.

In the early 1960's, emerging radio tracking technology allowed scientists to tag, track, and study land animals that were difficult to find in their remote habitats: Cochran (1975) followed a peregrine falcon, *Falco peregrinus*, from Wisconsin to Mexico, and Craighead and Craighead (1972) tracked grizzly bears, *Ursus horribilis*, going to their secluded wintering dens. Secretive animals dwelling in deep jungles, such as jaguars, could be radio-collared, and followed in their ranges, allowing much to be learned about their habits.

Biologists now could track, locate, and observe far ranging mammals in wide open spaces, such as Alaskan wolves (Mech, 1970) and moose (Van Ballenberghe, 2004). Soon many workers were following numerous animals. By March 1979, one of the leading commercial suppliers of radio-tracking equipment had sold over 17,500 radio collars (Mech, 1983). Because radio-tagged animals could be followed on foot, by land vehicle, or aircraft, animals could be followed long distances. When precise locations were obtained, and if the habitat was well understood, then much could be discerned and understood about the animals being studied.

The radio equipment and techniques for tracking land animals could not be applied to aquatic animals because of the strong attenuation of radio waves in water. However, acoustic tracking devices that could work underwater were soon developed, but the problem of attenuation of sound signals underwater could not be solved entirely. At first, the small sound emitting transmitters were externally attached to sharks; later they were surgically implanted into the coelomic cavity.

The early acoustic transmitters had short detection ranges, usually from 1–4 km, depending on location, sea condition, output power of transmitter, receiver used, etc. Because of these limitations, early acoustic tracking of sharks required remaining in close proximity to a shark to keep within detection range, an often difficult and arduous task from a small vessel. Thus, most of the early studies were carried out on sedentary or nonmigratory species, or on sharks which could be counted on remaining in the same area for prolonged times (such as juveniles in nurseries), and thus assuring detection.

One of the earlier shark tracking studies was carried out by Pittenger (1984) on Pacific angel sharks, *Squatina californica*, off California. In this study, 11 angel sharks were equipped with ultrasonic telemetry transmitters attached with "Floy" dart tags on the dorsal surface of the sharks. Transmitter life was 30–90 days, and detection from a boat ranged from 1 to 4 km. This shark is a sedentary species that often returns to the same spot during daytime, so its location was easy to find from day to day.

Morrissey and Gruber (1993) attached small ultrasonic transmitters into the coelomic cavity of juvenile lemon sharks, *Negaprion brevirostris*, in the Bahamas to study their home range. Despite the difficulties of tracking free-ranging large sharks from vessels, interesting studies were carried out. A megamouth shark, *Megachasma pelagios*, was tracked in its pelagic environment for 50 h by Nelson et al. (1997) and found to be a crepuscular vertical migrator.

Eventually, extensive hydrophones/receiver arrays would be built along the coastlines for the detection of tagged fishes, creating a network of passive detection devices that greatly facilitated the tracking of sharks. These networks allowed researchers

to produce studies, such as Heupel et al. (2003), which showed that tagged juvenile blacktip sharks, *Carcharhinus limbatus*, responded to a fall in barometric pressure associated with a storm by moving to deeper water.

The problems of following tagged animals by personnel or of animals leaving the area where the tracking receivers were located, were soon solved by satellite tracking technology. By 2005, tracking movements with satellite tags was the preferred method for shark research. These tags were relatively easy to use, and once implanted, the tag would record location, temperature, and depth. The tag could be programmed for release after a specified period of time, usually less than a year, depending on settings and battery life. The tag would then float to the surface and transmit the archived data to a satellite, and then the satellite would send the information to the researcher.

Although the method of tagging sharks with internal transmitters detected by underwater sensors continued to be used, satellite tags became the preferred method because sharks often traveled outside the areas covered by the sensors. Quite often the satellite tags failed to work, or produced little data, but sometimes these studies produced interesting results. When the tags were used in well-designed studies, and when they worked properly, the migratory movements of individual sharks could be followed in great detail, something researchers had never dreamed of even a few years earlier.

Satellite tag derived data demonstrated that the range of many shark species included entire ocean basins (Skomal et al., 2009; Campana et al., 2013), something that had been suspected for a long while (Castro, 1983), but not demonstrated. Shark tagging with satellite tags became immensely popular with the new generation of researchers.

As sharks became totemic[8] animals, tagging became the only acceptable research tool for many researchers who insisted on studying shark species solely by tagging. Necropsies of dead animals taken in fisheries became taboo or largely unacceptable (see below). Shark tagging became an endeavor and not just a research tool. In many projects there was no hypothesis tested or question to be answered, and sharks were often tagged with no knowledge of their sex or reproductive stage. Consequently, when results were obtained, sometimes the result was a set of disparate tracks which attested to the variability and complexity of behavior among different individuals, sexes, life stages, etc., and it was difficult to discern or understand movement patterns.

Another problem of tagging endeavors is the expectation that something other than movements can be discerned from the tagging data. Unlike terrestrial habitats, the ocean realm and marine habitats are not sufficiently known to infer what the animal may be doing in a given area. It is certain that future tags will be more complex and productive, and there is much guesswork of what can be done by "more intelligent tags" which can sense the physiology or behavior of the animals. At this time, this is mere speculation, and such "intelligent" tags remain to be developed.

The Third Factor: The Rise of the Shark Fishery and the Fishery Management Plan

In 1972, after some 25 years of open antagonism and hostility between the United States and The People's Republic of China, and after extensive diplomatic negotiations, President Richard Nixon visited China. This was the first step in the normalization of relations between the two countries. During the next two decades, complex economic and financial ties developed steadily between the two countries. In due time, the combination of Chinese energy and cheap labor and American capital and know-how, made China the manufacturing colossus of the early twenty-first century.

China's economic boom, beginning in the late twentieth century, improved the standard of living for some segments of the Chinese population. A greater proportion of their society was able to afford luxuries that had previously been out of reach. One of those luxuries is shark fin soup. In China, a soup utilizing the fibers (ceratotrichia) found in shark fins has been a symbol of prosperity and health for centuries. The dish is a demonstration of wealth and class served at special occasions such as weddings.

Soon after the establishment of diplomatic relations between the United States and China, American and Chinese merchants were figuring out what businesses could be conducted with each other. At this time, the new Chinese and Asian economic prosperity caused the demand for shark fin soup to increase substantially. Thus, when Chinese merchants expressed a growing demand for shark fins, American entrepreneurs sought to fulfill it.

Sharks were one of the few fish resources not targeted or fully utilized by U.S. commercial fisheries. While there was a strong U.S. recreational shark fishery, in general, the commercial fisheries had not impacted sharks since the late 1940's. The only exceptions were porbeagle sharks, *Lamna nasus*, that were targeted in the early 1960's off New England (Campana et al., 2001).

Shark stocks in southeastern U.S. waters were relatively high because they had not been fished since shark liver oil was in high demand in the 1940's, with the exceptions of dusky sharks, *Carcharhinus obscurus*, and oceanic whitetip sharks, *Carcharhinus longimanus*, which were taken incidentally in large numbers in Japanese tuna fisheries in the Gulf of Mexico in the 1960's.

It took about a decade for business and financial channels to develop, and by the early 1980's substantial changes had occurred in demand for shark fins. China's rising standard of living and new wealth increased demand, and the demand resulted in higher prices paid for shark fins. This encouraged American fishermen to enter the shark fishery. Tuna and swordfish fisheries

[8]See later section on sharks as totemic creatures.

that previously had discarded sharks (dead or alive) now began seeking the fins. However, low prices paid for the meat resulted in fishermen just removing the fins from sharks and discarding the carcasses into the ocean, thus saving freezer space for the more lucrative tunas and swordfish. This wasteful practice became known as "finning" (NMFS, 1992).

The Magnuson-Stevens Fishery Conservation and Management Act (MSFCMA) is the primary law governing marine fisheries in U.S. federal waters. First passed in 1976, the MSFCMA was written to prevent overfishing, rebuild overfished stocks, and increase the long-term economic and social benefits of the fisheries. It extended U.S. jurisdiction to 200 nmi from its coasts. Prior to the MSFCMA, waters beyond 12 nmi were international waters and could be fished by fleets from other countries. It also established eight regional fishery management councils (FMC), which develop fishery management plans for their respective jurisdictions.

Shortly after the MSFCMA passed in 1976, the Mid-Atlantic Fishery Management Council started work on a shark fishery management plan but stopped owing to inadequate information. Through the 1980's shark catches increased due to the demand for fins and meat. In just one decade, U.S. commercial shark landings grew from 135 t in 1979 to 7,172 t in 1989 (NMFS, 1992). Both conservation organizations and regulatory agencies became concerned about the rapid growth of the unregulated shark fishery.

One of the first organizations to notice and act on the rapidly growing, uncontrolled shark fishery was the Gulf of Mexico Fishery Management Council (GMFMC), based in Tampa, Fla. Lacking the knowledge and data on sharks needed for management, the GMFMC requested bids from environmental companies to write a first draft of a management plan for sharks.

The first draft of the "Fishery Management Plan for Sharks and Other Elasmobranchs in the Gulf of Mexico" was issued in February 1979 by the GMFMC. It had been prepared by Environmental Science and Engineering, Inc., the company that had won the competitive bid for the plan.

A more comprehensive "Draft Fishery Management Plan/Environmental Impact Statement/Regulatory Analysis" was issued jointly by the GMFMC and NMFS in September 1979. This last publication outlined the management objectives: minimize the bycatch of species other than sharks by foreign fisheries, maximize the benefits derived from fishing by domestic fishermen from sharks and other elasmobranchs, minimize conflicts among participants in the shark fishery, and establish a data collection system for future management of the fishery. Conservation of sharks was not an objective of this draft plan, but several more drafts of the plan soon followed.

Because many species of economically important sharks are migratory and cross several jurisdictional boundaries in their seasonal migrations, the five east coast FMC's (New England, Mid-Atlantic, South Atlantic, Gulf of Mexico, and Caribbean) recognized the need for a unified Shark Fishery Management Plan. On 3 June 1989, the five councils requested that the Secretary of Commerce develop a fishery management plan for the shark fishery. Their concern was that it would take too long for the five councils to develop their own individual plans, and that, in view of the rapidly growing fishery, the delay could cause irreparable damage to shark stocks.

A team of NMFS personnel (including the author of this article) was assembled in 1989 to prepare a management plan for sharks of the U.S. east coast. NMFS had limited data on shark catches, and what existed was not broken down by species. Personnel attempted to obtain data on shark landings from the commercial industry. Few data sets were available because, in general, fishermen did not record the information needed for stock assessment purposes (e.g., landings by species, catch per unit of effort, etc.) or for the regulation of the fishery.

A few data sets were obtained, notably from fishermen Chris M. Brannon of Bayou La Batre, La., and Eric Sander of Daytona Beach, Fla. After much work and consultations, a shark fishery management plan was prepared (NMFS, 1992) and published on 10 Dec. 1992. The plan was data-deficient for the above cited reasons, and some of its predictions would prove wrong. But the key to its success was a provision for change and improvement by designating an "Operational Team" which could amend the plan's regulations and quotas as new data were obtained. Over the next two decades the plan was emended and amended many times.

The plan not only protected shark stocks by restricting both recreational and commercial fisheries, but it ushered in a new era of research on sharks. NMFS needed shark data upon which to base shark regulations. Landings by species information was needed, and that meant that fishermen, dealers, and enforcement agents had to be able to identify species within the catches. Management agencies needed reports on catches, and assessment of the stocks had to be carried out. The councils and granting agencies made shark research a priority, and funds for shark research flowed through programs such as Marine Fisheries Initiative (MARFIN) and the Saltonstall-Kennedy (S-K) Grants Program.

In the 1990's, scientific and public interest on sharks and the availability of research funds resulted in the appearance of shark research groups. In 1990 the Bimini Biological Field Station was established by Samuel Gruber of the University of Miami. In 1992 a consortium, involving personnel from Mote Marine Laboratory in Sarasota, Fla. (under Robert E. Hueter); Moss Landing Laboratory, at Moss Landing, Calif. (under Gregor Cailliet); Virginia Institute of Marine Science at Gloucester Point, Va. (under John A. Musick); and the University of Florida in Gainesville, Fla. (under George Burgess) was "established by the U.S. Congress" and named the National Shark Research Consortium.

The group was funded through political "earmarks" for a number of years.

In 1993, a Shark Research Group was established at the Hawai'i Institute of Marine Research (under Kim Holland) in Kane'ohe Bay, Oahu. In 1998, a Canadian Shark Research Laboratory, at the Bedford Institute of Oceanography in New Brunswick, was established by Steven E. Campana. In the same decade, many conservation organizations set up shark conservation programs with officers dedicated to those programs, and they became quite active in drafting protective legislation.

Most of these groups flourished in the late 1990's and early 2000's because of the combination of talent and available funds. However, by 2015, much of the institutional interest in sharks had waned, and due to lack of funding (e.g., loss of "earmarked" money), or retirements, most of the research programs were greatly reduced, some groups being reduced to an investigator and an assistant, often on soft money. One of the most productive programs, the Canadian Shark Research Center, had ceased operations due to its leader taking a position elsewhere.

Similarly, the interest of the large conservation organizations in shark conservation and programs only lasted through the heyday of shark conservation and had waned by 2010, when many organizations had abandoned their shark programs and moved on to other endeavors. Legislation protecting sharks had been enacted in the United States, and the fisheries had been curtailed. Other countries and the United Nations had passed legislation or protocols for the protection of shark stocks. However, the protection was very limited or mainly illusory. Unregulated shark fisheries continued to kill untold numbers of sharks to supply fins for Asian markets, with the basic problem being the killing of sharks on the high seas and in coastal zones of countries where law enforcement did not exist. These were very tough, long-term problems that few conservation organizations could or wanted to tackle. The era of the shark research laboratories and the big-organization shark conservation movement was essentially over.

The Fourth Factor: The "Jaws" Phenomenon

In 1974, Peter Benchley's great novel, "Jaws," was published, followed a year later by the movie of the same title. Directed by Steven Spielberg, the movie became one of the most influential in history. "Jaws" affected the behavior and attitudes of millions of people towards sharks and the ocean, and the effects lasted for several decades. The effects of the movie were so deep, varied, and long-lasting that they eventually encompassed totally opposite behaviors.

The movie "Jaws" is a modern "Moby Dick" story (Melville, 1879) and there are remarkable parallels between the two novels. Both novels revolve around very large specimens of their kind, a huge white sperm whale, *Physeter catodon*, and a huge white shark. In both works, the human protagonist is a boat captain bent on revenge against the sea monster. Also in both novels, after a prolonged chase, in the final encounter, the monster rams the vessel, the captain is entangled in the ropes and is dragged to his death, and the monster then dies. The lone survivor, buoyed by flotsam, survives.[9]

There is also a similarity between the movie plot and actual events in 1916, when a series of shark attacks along the New Jersey shore, caused town fathers to try to downplay or keep them secret so as not to ruin the local tourist season. McCormick et al. (1963:15) recount that "After losses estimated at $1,000,000 in canceled reservations, the mayors of 10 New Jersey resort towns met at Beach Haven, where the first shark attack had occurred, and pleaded for an end to the panic. They asked newspapers to refrain from publishing stories that 'cause the public to believe the New Jersey seacoast in infested with sharks, whereas there are no more than in any other summer.'"

Melville's 1851 novel "Moby Dick" was originally a commercial failure (Maxwell, 1986), and so was his writing career. In difficult financial circumstances after "Moby Dick" was published, Melville became a customs inspector for the last 20 years of his life, and died in obscurity in 1891. "Moby Dick" was not considered as one of the "greatest American novels" until the mid-twentieth century. By contrast, Benchley's novel and the subsequent movies based on the novel were great financial successes, and the effects of the original movie were significant and felt for many decades.

Why did the movie have such impact and why did it have such diverse and long lasting effects? The first reason was the vivid, unforgettable scenes. The mechanical shark used for filming "Jaws" is seldom seen in the film; and when the shark does appear, it is not very realistic. The mechanical shark, said to have been a trouble-prone device for the film crew, was used sparingly but still most effectively.

The scenes terrified movie-goers, despite the obviously fake shark and lack of the constant blood and gore of present-day high-tech movies. Countless children and many adults were fascinated, or traumatized, by the image of the voracious man-eating shark. As a result, sharks would be perceived as malevolent, man-eating creatures for several decades. Three or four decades after the release of the film, many movie-watchers would recall the powerful images every time they entered a beach. Others told the author that the catchy "Jaws" tune still plays in their heads whenever they enter a beach.

The movie had other unexpected long-term effects. In a country where fiction depicted on movies or television screens is easily taken for truth by a gullible public, the movie set off a shark killing frenzy that lasted nearly two decades. Sport fishing for sharks had gained popularity in the 1960's. Shortly after the movie appeared, shark fishing as a sport increased

[9]In the movie "Jaws," there are two survivors; one in the original novel.

greatly, and in the next decade, dozens of shark fishing clubs and tournaments sprang up along the U.S. east coast. These tournaments were often held monthly during the summer at many seaside locations, from New York to Florida (Fig. 3).

The movie caused such antipathy toward sharks that some tournaments had prize categories for "the most sharks caught" and the "greatest number of pounds of shark landed." Emulating Quint, the fisherman in "Jaws," shark fishermen saw themselves as heroes ridding the seas of dangerous sharks.

In 1990–91, this author participated in the public hearings conducted during the preparation of the shark fishery management plan, which would place restrictions on the rapidly growing shark fishery. Commercial shark fishermen, opposing the enactment of legislation, often claimed that any restrictions on their fishery would result in dozens of shark attacks in coastal waters, their logic based on what they had seen in the "Jaws" movie.

This unfortunate attitude and ecological havoc persisted for nearly two decades. The ecological effects of the removal of large numbers of predators from the environment were not studied or recorded, because of the limited understanding of the biology of sharks and their ecological relationships. The U.S. recreational shark catch increased from 265,000 sharks in 1981 to a high of 746,600 sharks in 1983. After that year, the catch started to slowly diminish, and it had decreased to 66,300 sharks by 2004 (Cortés and Neer[10]).

Figure 3. Shark fishing tournament, Port Salerno, Fla., Sept. 1986. Large crowds came to view the dead sharks.

Shark Television

The movie *Jaws* also engendered a new television genre. In 1988, the public fascination, or obsession, with sharks caused by the movie led the "Discovery Channel" to produce "Shark Week," a week-long series of programs based on sharks. The shows were instantly successful. In time, "Shark Week" would become the longest-running program on cable television, having lasted 28 years as of 2016.

In the early years, the shows were loosely based on natural history or conservation of sharks and were fairly realistic. Perhaps catering to what was attractive to the audience, programs soon became centered on white sharks or bull sharks, *Carcharhinus leucas*, and their attacks on people. Eventually, one show descended to toothy mechanical sharks propelled against watermelons filled with a red fluid. When hit by the mechanical sharks the watermelons exploded, splashing red fluid in all directions, a cinematographer's concept of a shark attach that could not fail to impress little children.

As satellite tags were developed and became widely used, filmmakers turned to shark tagging to replace the

[10]Cortés, E., and J. Neer. 2005. Updated catches of Atlantic sharks. SEDAR (Southeast Data Assessment and Review) 11, Doc. LCS05/06-DW-16, NMFS Panama City Lab., Southeast Fish. Sci. Cent., NOAA.

superannuated shark attack programs. The tagging of a large shark is always an exciting event and could produce the action footage that the networks loved. Because of the high cost of satellite tags, film producers could always find a willing researcher lacking funds or seeking publicity, although most of the time the "researchers" were usually unknown to those actually studying sharks. The "researcher" could assume heroic poses in the tagging film, which could be finished with the perennial "high fives" of such films. The networks loved it!

Tagging white sharks with satellite tags soon became a favorite subject of film producers and networks because it could be made into television programs complete with websites dedicated to tracking the tagged sharks. The public could then view the movements of a given white shark along the coast. Although more in the realm of entertainment than research, these programs served to educate the public that white sharks roamed our coasts and interacted with swimmers only infrequently.

In efforts to improve their ratings, some network programmers shifted more toward entertainment and "docufiction," where fiction was presented in the manner of documentaries. The first of these programs presented the discovery of mermaids (on "Animal Planet" in June 2012), and it was so "successful" that others of that ilk soon followed. Another piece of "docufiction" followed in "Shark Week" in August 2013, a program titled "Megalodon: The Monster Shark Lives," supposedly demonstrating the existence today of the extinct giant shark, *Carcharodon megalodon*.

These faux-documentaries, which included interviews with supposed experts (really actors), were somewhat confusing and misleading. But the presentation was so "effective" that it fooled naive adults and even some educated people into believing in the existence of giant sharks. School teachers at times called the author asking how to counteract these programs that confused their pupils.

The Rise of "Personal Shark Conservation Groups"

The most significant impact of "Jaws" was caused by the character "Matt Hooper," the irreverent shark biologist played by Richard Dreyfuss. This character, and its personification, would have a profound and long-lasting effect on the young audience, for it told them that there was such a profession as "shark biologist" and that one could have a career studying sharks.

Kids who saw the film often fantasized about being shark biologists. They were motivated by the imaginary social aspects of being a shark biologist, and their interest in sharks was often confined to the white shark. Years later, many would pursue careers in shark biology, and many of the people in shark biology today attest to seeing the movie and then deciding that they would be shark biologists. Unfortunately, the sad reality was that there were very few positions available in shark research.

A small number of the newly trained biologists found niches in academia, where they could pursue their research interests on sharks when their teaching load or grant money allowed. A smaller number would find employment in the government agencies or contract research companies conducting fishery research or sampling. Others, sometimes lacking the traditional training in biology or other sciences, would opt for careers in conservation or management, but sharks would remain their main interest.

Some would wait years for an academic or government position in shark research to become available or to be offered to them, often working on soft money or adjunct positions at institutions that would give them a desk and an adjunct title only if they brought grants that would pay for the overhead or rent. Yet others would work, in positions well below their qualifications, for many years to support their avocation, such was their commitment to their endeavor.

The flood of young people, influenced by the movie and determined to "do something with sharks," or wanting "to study behavior of white sharks," and searching for jobs with shark conservation groups far exceeded the number of positions or funding available in the large, well-established organizations. Thus, for many people there was only one way to self-actualize or to achieve their goals of "doing something" with sharks: to create one's own organization, or team up with similarly minded folks or a few acolytes, and create a new shark conservation group.

The result was the formation of a large number of shark conservation or protective groups, and a brief Internet search revealed dozens, if not hundreds, of such entities. The size of the organizations is quite variable; a few are large groups, many others are composed of only a few people, sometimes only one or two, with a web site. Their members may seldom interact with the scientific community, but some offer educational websites of varying quality. They often deliver their shark conservation message to children in grade schools, where teachers are only too glad to have someone come in and entertain their charges.

The Rise of Sharks as Totemic Animals

A common trait and peculiar aspect of many young people who, influenced by the movie "Jaws," wished to become shark biologists, was their general lack of interest in biology or natural history. This was surprising, because curiosity about animals or their natural history has always been the sine qua non of biologists. However, my many personal observations and conversations with shark-enthusiasts revealed that many were not interested in the natural history of sharks or any other animals. (Knowledge of natural history is necessary to ask the questions that provide hypotheses that can be scientifically tested.) To them sharks were attractive and "cool" animals rather than objects of scientific curiosity.

While based at a marine laboratory for well over a decade (2000–2013), I

often brought rare sharks to the laboratory for examination. I used to announce to scientists and interns when I would have the shark available for viewing and when a necropsy would be performed. Hardly anyone ever came to see these rare fishes. When interns came, they came briefly, just long enough to take a "selfie" next to the shark, and left without bothering to examine it.

In a decade or two (~1995–2010), an unusual transformation occurred in the perception of sharks. In the society, sharks went from being feared animals to protected and even totemic animals. In the shark-enthusiast community, the combination of interest or mild obsessions with sharks, the desire to do something and protect sharks, and mysticism, resulted in sharks becoming totemic animals. Even for some in the field of ichthyology, sharks ceased to be "fishes" and became totemic animals.

Totemism is a complex social phenomenon where individuals or groups form a mystical or emotional relationship with a venerated or sacred object, the totem, usually an animal. Totemism was once considered a stage of religion through which all societies must proceed, a stage where animals, plants, and heavenly bodies were conceived as gods, before the advent of anthropomorphic gods (M'Lennan, 1869–70; Frazer, 1887).

Today, totemism, with its symbolism, is viewed as a culturally variable phenomenon (Levi-Strauss, 1963), and not as a general stage of man's cultural development (Haekel, 1986). I use the concept of totemism here because the behavior of many people towards sharks matches nearly all the characteristics of totemism given by ethnologists, and because of lack of a better concept to explain the facts.

As M'Lennan (1869–70) stated "what the Totem is cannot be conveyed in one sentence...and we must go somewhat into details." A survey of the literature on totemism (Radcliffe-Brown, 1965; Haekel, 1986) reveals some common characteristics to totemic phenomena:

1) There is an emotional relationship between a person, or group, and an animal (a kind of animal or a species), the totem.
2) The totem is sacred and revered, venerated, admired, or viewed with awe.
3) There is usually a prohibition (taboo) against killing, eating, or even touching the totem, especially if it is dead.
4) The totem may be a protector or may be protected.
5) Totemism often involves the use or wear of totemic emblems or designs.
6) The person, or group, shares the totem with other members of the group or clan.
7) Organization into totemic clans with defined rules of kinship and exogamy.

Most of the literature on totemism dates back to the late 19th or the early 20th centuries, when Europeans were learning about the "primitive" cultures they were destroying.[11] A form of totemism is common in modern societies, in the naming of sports teams, where aggressive animals are chosen as the totem, the animal's name is taken for the group or clan, and their totemic emblems are worn or displayed by members of the group.

As one would expect, the white shark became the most totemic of sharks. As such, it became the icon and the subject of many articles: from a yearly average of 2 articles on white sharks a year in "Zoological Record" during 1975–79, to an average of 5.8 articles a year during 1980–89, to an average of 32 articles a year in 2010–15, with a record 64 articles in 2015 (Fig. 4). Some authors published voluminously on the white shark, one author alone accounting for 10 (45%) of the 22 articles on white sharks published in 2004 of varying import.

The taboo against killing, eating, or touching the totem caused a change in the methods used to investigate the biology of sharks. Necropsies had been the foundation for most shark research and knowledge for decades. However, because the taboo included touching dead sharks, shark necropsies became unacceptable to many shark enthusiasts. Although research specimens could be easily obtained from the fisheries, as sharks continued to be fished for or were taken as bycatch, few of the enthusiasts would consider complementing their researches with necropsies. Other researchers have reported this taboo against killing sharks.

Heupel and Simpfendorfer (2010: 1213) wrote "Growing concern for shark populations appears to be increasing pressure not to kill these animals. This raises concern about how research on sharks is regarded and implications of publicity on the decline in shark populations. One noticeable result of the increase in concern about sharks is that more students inquiring about graduate school who are interested in working on sharks are indicating that they are not willing to participate in projects that may harm sharks. This occurs before they know which species are involved, the status of that species, or what benefits could be gained from lethal sampling. This suggests their perspective is not rooted in science, but is ethical, political, or emotive." Similarly, at a recent meeting of the American Elasmobranch Society (2016), the emphasis on using "non-lethal methods" was so great that speakers felt it necessary to state that "no sharks were harmed in this investigation."

Thus, tagging, DNA analysis, and stable isotope analysis became fashionable and the only acceptable modes of research for the shark enthusiasts, because these could be accomplished without violating the taboos. Taking a "fin clip" or blood samples from live animals were the only samples permissible. This meant that the diet of

[11]The topic seems to have gone out of fashion with ethnographers. Most of the recent literature consists of discussions or footnotes on Levi-Strauss (1963). According to Levi-Strauss, the term totemism covers only cases in which there is "a coincidence of" 1) a frequent identification of human beings with plants or animals, and which has to do with very general views of the relations between man and nature; 2) a designation of groups based on kinship, which may be done with the aid of animal or vegetable terms, but also in many other ways.

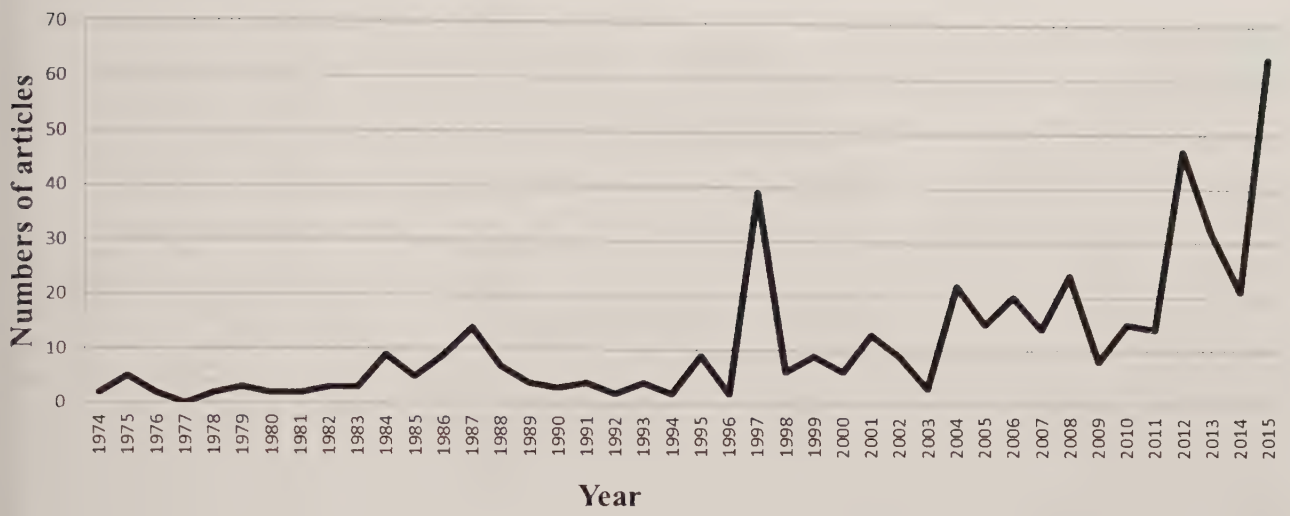

Figure 4. —The number of articles on the white shark per year 1974–2015. The peaks of 1986, 1996, and 2012 were caused by the publication of the white shark symposia. The peak for 2015 cannot be attributed to such cause.

sharks could only be analyzed through stable isotope analysis, with all the vagaries of the method, even when stomach contents analysis could be easily performed in specimens freely available in local fisheries.

In true totemic fashion, enthusiasts or clan members wear shark shirts, hats, pins or have tattoos of sharks (Fig. 5). They adopt names such as "Shark man" or "Shark Lady" or common names of shark species, e.g., "mako girl." Their calling cards invariably depict a shark.

Shark Biology Becomes Shark Advocacy

When sharks ceased to be "fishes" and became "totemic animals," much of shark biology evolved into advocacy. Although there were sufficient scientific, ecological, and economic reasons to protect sharks, a totemic relationship requires that the totem be protected and be a protector of the clan. Thus, it was necessary, in the advocates' view, to dispel "the myths created by Jaws," or the idea that sharks are, or could be, man-eaters.

The notion of sharks as man-eaters was not compatible with the relationship desired with the totemic animal. Furthermore, if sharks were man-eaters, or potential man-eaters, they would not be tolerated and could not be protected in a society where most people are not aware of the differences among domesticated, tamed, and wild animals. So, in the advocates view, totemic sharks could not be man-eaters. Thus, a change in perception was needed, and sharks had to be portrayed as harmless to humans.

One example of this desired change in perception is illustrated by the article by Neff and Hueter (2013), where they proposed "reclassifying human-shark interactions." These authors pointed out that there were different types of shark attacks and that the term "shark attack" carried the perception of fatal outcomes and was "outmoded." These authors suggested that human-shark interactions that resulted in fatalities should be termed "fatal shark bites" and that "the term 'shark attack' be avoided by scientists, government officials, the media, and the public, in almost all instances of human-shark interaction." Based on the response in many Internet sites, the idea was warmly received by many shark enthusiasts and advocates.

To attack is to set upon with sudden violence or force. Animals, domestic, tamed, and wild, can and do attack people (pit-bull terriers being a main culprit these days, accounting for a fatality every 21 days in the United States[12]). Attacks on humans by sharks are rare. The ranges of sharks and humans overlap only occasionally, in the beaches and coastal zones during people's leisure activities or in the open ocean after shipwrecks or the ditching of an aircraft. The causes of these attacks, varied and difficult to predict, have been described by Baldridge (1974) and need not be reviewed here.

Most situations of injuries to humans by sharks, called "shark attacks," are just bites. When a surfer's hand gets slashed by a shark, or when a man gets bitten while feeding sharks, it should not be classified as an attack. To call such events "attacks" is inaccurate and wrong, as Neff and Hueter pointed out, and an example of poor logic or reporting.

Similarly, when a person is swimming off a beach, or a ship-wrecked sailor is floating in the ocean, and is attacked by a large shark and maimed, killed, or devoured, it would be inaccurate and misleading to call that a "bite" or even a "fatal bite." Those terms are

[12]For statistics on fatal dog attacks in the United States see DogsBites.org.

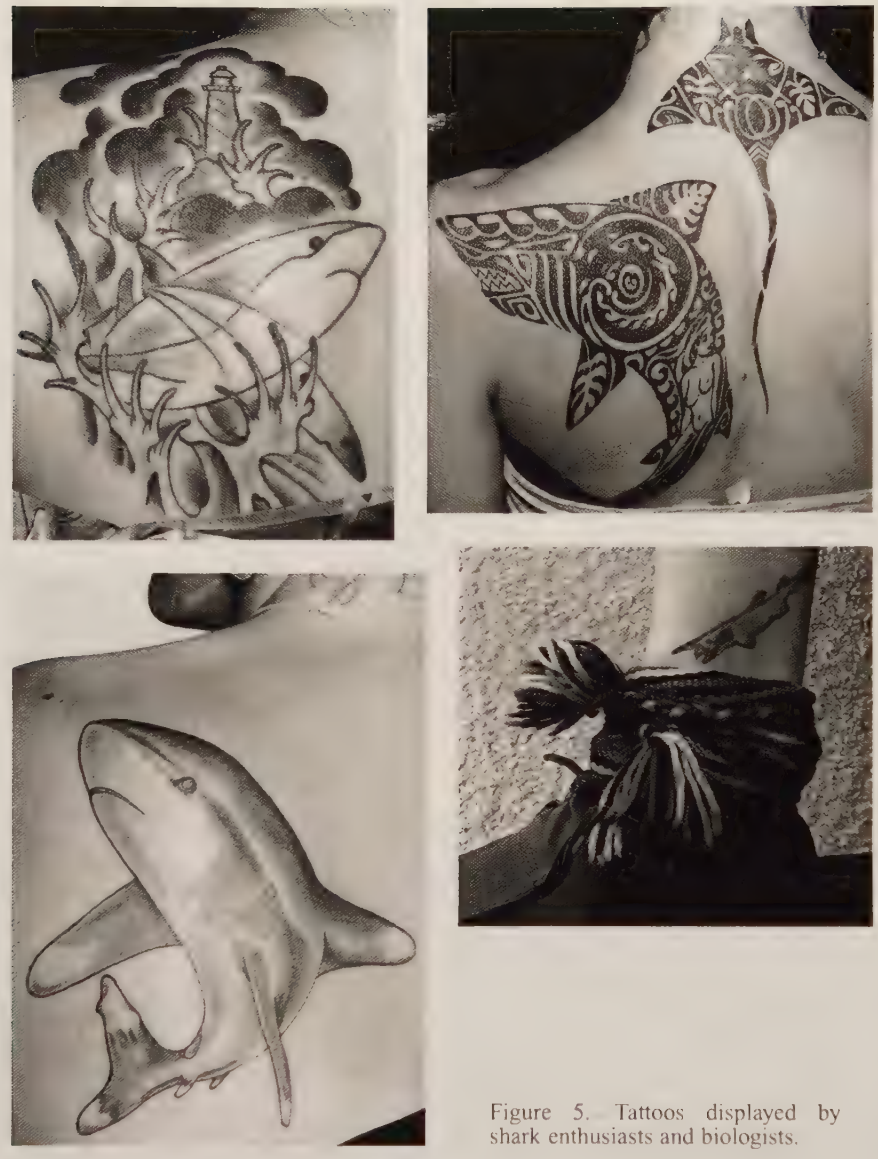

Figure 5. Tattoos displayed by shark enthusiasts and biologists.

best used for interactions with creatures such as venomous snakes.

When a person steps on a cobra and gets bitten, it is referred to as "a bite" or "a fatal bite." No one refers to it as "a cobra attack." One must also note that in cases where crocodiles or bears attack and consume people, no one is suggesting that those attacks be termed "fatal crocodile bites" or "fatal bear bites" because those animals, although potential totems, are not totemic animals today.

Shark Literature in the Age of Advocacy

In an eloquent essay about fisheries in general, Hilborn (2006), noted the encroachment of advocacy into fisheries science: "This faith-based fisheries movement has emerged in the last decade, and it threatens the very heart of the scientific process-peer review and publication in the top journals...I assert that the peer review process has now totally failed and many of these papers are being published only because the editors and selected reviewers believe in the message, or because their potential newsworthiness...Critical peer review has been replaced by faith-based support for ideas and too many scientists have become advocates."

The problems of the shark literature in the Age of Advocacy are compounded by the lack of qualified reviewers, a perennial problem of the shark literature (Castro, 2011), and by the imposition of so-called "ethical standards" by editors. Today the logistics of shark research continue to be difficult, and with many researchers limiting their methodologies to tagging or getting blood samples, there are fewer researchers with the broad experience and technical expertise needed to properly review papers.

The increase in the numbers of journals that has occurred in the last decade, due to the rise of online journals, has resulted in greater competition for articles and for readers. These factors lead some editors to seek articles that will meet the advocates' approval, and to use unqualified reviewers who share their ideologies, and who are too happy to be considered qualified for the task. Examples are given below:

The cover of "American Scientist" of the March–April 2014 issue bears a photograph of a diver and a whale shark, *Rhincodon typus*, with the headline "Can tourism save the whale shark?" The author states, "The hunting of the whale sharks for their meat and oil-rich livers was once globally wide-spread although this practice has now largely stopped. Like other elasmobranchs...whale sharks have slow growth rates and reach sexual maturity late, making them particularly vulnerable to overfishing." And, "Evidence for declining catches over the past 15 to 20 years has placed the species on the Red List of Threatened Species, generated by the International Union for Conservation, and on the appendixes for several international conservation conventions." (Davies, 2014:118).

Is the whale shark threatened by any fishery? In reality there have been

few fisheries for whale sharks. There have been none in the Western Hemisphere, and the ones from the Eastern Hemisphere (Taiwan, India, Philippines) have been small and localized. None operate today, although a few whale sharks are probably taken at remote locations by tribesmen in the Philippines.

Contrary to the implication of the statement of the species being "on the Red List of Threatened Species," the whale shark is listed only as "Vulnerable," a play on words to make the species appear threatened and support the author's unwarranted statements. To my knowledge, the oil of the whale shark has never been utilized commercially (although there was an unverified Internet report of use by the Chinese in 2014).

And the whale shark is one of the fastest growing sharks although the age at maturity is unknown. The "evidence" for declines must refer to one site in Taiwan, a fishery that operated in the 1990's and closed in 1998. Whether such lapses are due to researchers attempting to make their work appear novel, their ignorance or that of reviewers or editors, or the article agreeing with the ethical standards or marketing goals of the editors is unknown.

Another characteristic of the new publishing is the presentation of old knowledge as if it were new. For example, a 2013 article by Oliver et al. (2013) in "PLOS One," bears the title "Thresher sharks use tail-slaps as a hunting strategy," and concludes "The evidence is now clear; thresher sharks really hunt with their tails." The article is based on observations and films of threshers attacking prey. However, the fact that thresher sharks do use their tails to slap and stun prey has been known with certainty for nearly a century.

Allen (1923) provided a good description of a thresher shark using its tail to stun fish. And most modern books on sharks or shark biology refer to thresher sharks using their tail to obtain prey, e.g., "These sharks use their long, powerful tails to stun prey with sharp blows (Castro, 1983); "The caudal fin is also used as a whip to stun and kill prey, and threshers are commonly tail-hooked on longlines after striking the bait with the caudal tip" (Compagno, 1984); "Prey are rounded up near the surface and stunned by the shark's thrashing tail" (Last and Stevens, 1994).

Figure 6.—Postcard from the early 20th century, said to be from the St. Petersburg, Fla., area, that demonstrate the idea of harnessing sharks as if they were aquatic horses.

There is also a long review of the knowledge of the use of the tail in prey capture by thresher sharks in Castro (2011:243–245). Were the authors or reviewers ignorant of the fact that thresher sharks use their tails to kill prey?

Shark Research Today

Most of the logistical difficulties of the past are still with us, and shark research continues to be difficult. Today, much research is mainly concentrated on a few species of sharks, such as the totemic white shark and the "charismatic" whale shark. We have had countless articles on the white shark, and three symposia dedicated to the species in 1983, 1993, and 2010, resulted in three comprehensive publications (Sibley, 1985; Klimley and Ainley, 1996; Domeier, 2012a). But, despite more than 30 years of enthusiastic research attempts on these and a few other species, our knowledge is still fragmentary.

We have learned much about the migrations of white sharks in the northeastern Pacific through tagging in the last decade (for a summary see Domeier, 2012a). We know that U.S. west coast white sharks often travel to an area between the California coast and Hawaii that has been named the "Shared Offshore Foraging Area"[13] (Domeier, 2012b), but we do not know why. We have a generalized idea of where its west coast nurseries are, but where are the gravid females? We know little of its reproductive processes, and we still do not know its reproductive cycle or gestation period: "current estimates of gestation are guesses based on very little empirical data" (Domeier, 2012b:217). Age at maturity and longevity estimates vary widely, and always increase with the latest estimate. We know that white sharks usually die suddenly in captivity, but we do not know the physiological reason. Of the U.S. east coast population we know little. We do not even know where it gives birth (probably in the northern Caribbean).

[13]Also dubbed "the white shark café."

Of the whale shark, we know much less, and what we know was learned several decades ago. We do not know its life history, age at maturity, longevity, reproductive cycle, gestation period, migration patterns, location of its nurseries, physiology, etc. Yet, while so many researchers concentrate on the white shark or the whale shark, many other interesting or commercially important species are ignored, such as the ubiquitous shortfin mako, *Isurus oxyrinchus*.

Given the present reliance on tagging as the main research tool, it is unlikely that we will soon acquire a reasonable knowledge of the life history of the shark species we investigate or answer the many questions that exist about them. And it is unlikely that the emphasis on tagging sharks will change until the television stations and the public tire of programs of people tagging sharks.

Perhaps new tags will be developed that can increase our knowledge of these animals, but this remains to be seen. However, given the present trends, it is likely that progress will be slow until the field returns to scientific methods and hypothesis testing, and methodologies are aimed to answer the specific questions asked about these great fishes.

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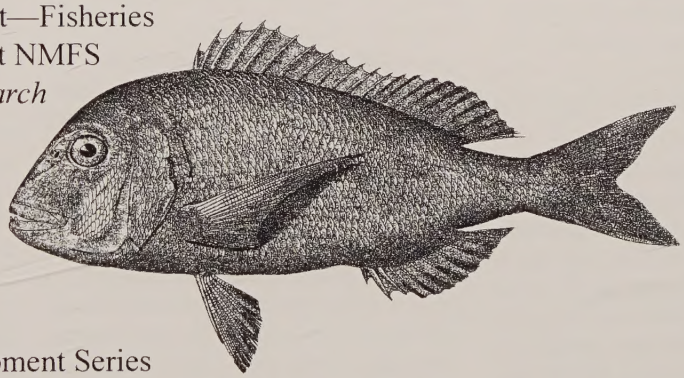

Editorial Guidelines for the *Marine Fisheries Review*

The *Marine Fisheries Review* publishes review articles, original research reports, significant progress reports, technical notes, and news articles on fisheries science, engineering, and economics, commercial and recreational fisheries, marine mammal studies, aquaculture, and U.S. and foreign fisheries developments. Emphasis, however, is on in-depth review articles and practical or applied aspects of marine fisheries rather than pure research.

Preferred paper length ranges from 4 to 12 printed pages (about 10-40 manuscript pages), although shorter and longer papers are sometimes accepted. Papers are normally printed within 4-6 months of acceptance. Publication is hastened when manuscripts conform to the following recommended guidelines.

The Manuscript

Submission of a manuscript to the *Marine Fisheries Review* implies that the manuscript is the author's own work, has not been submitted for publication elsewhere, and is ready for publication as submitted. Commerce Department personnel should submit papers under a completed NOAA Form 25-700 (available from the SPO website).

Manuscripts must be double-spaced throughout, and a complete manuscript normally includes a title page, a short abstract, text, literature citations, tables, figure legends, footnotes, and the figures. The title page should carry the title and the name, department, institution or other affiliation, and complete address (plus current address if different) of the author(s). An "Acknowledgments" section, if needed, may be placed at the end of the text. Use of appendices is discouraged.

Abstract and Headings

Keep titles, headings, subheadings, and the abstract short and clear. Because abstracts are circulated by abstracting agencies, it is important that they represent the research clearly and concisely. Headings within each section must be short, reflect a logical sequence, and follow the rules of multiple subdivision (i.e., there can be no subdivision without at least two items).

Style

The entire text should be intelligible to interdisciplinary readers; therefore, all acronyms, abbreviations, and technical terms should be spelled out the first time they are mentioned. The scientific names of species must be written out the first time they are mentioned; subsequent mention of scientific names may be abbreviated. Follow the U.S. Government Printing Office Style Manual (2008 ed.) and the Scientific Style and Format: the CSE Manual for Authors, Editors, and Publishers (2014, 8th ed.) published by the Council of Science Editors.for editorial style, and the most current issue of the American Fisheries Society's Common and Scientific Names of Fishes from the United States and Canada for fish nomenclature. Only journal titles, scientific names (genera and species), and vessel names should be italicized. Dates should be written as follows: 11 November 2013. Measurements should be expressed in metric units, e.g., metric tons as (t); other equivalent units may also be listed in parenthesis. Common abbreviations and symbols such as mm, m, g. ml, mg, and °C (without periods) may be used with numerals. The numeral one (1) should be typed as a one, not as a lower-case el (l). Write out the numbers zero through nine unless they form part of measurement units (e.g., nine fish but 9 mm).

Footnotes

Footnotes should not be embedded within the text document. They must be numbered with Arabic numerals and listed separately. Footnote all personal communications, unpublished data, and unpublished manuscripts with full address of the communicator or author, or, as in the case of unpublished data, where the data are on file. Authors are advised to avoid references to nonstandard (gray) literature, such as internal, project, processed, or administrative reports, wherever possible. Where these references are used, please include where they may be located (website or public depository).

Tables

Tables should be printed separately and double-spaced. Tables should not be excessive in size and must be cited in numerical order in the text. Headings should be short but ample enough to allow the table to be intelligible on its own. All unusual symbols must be explained in the table heading. Other incidental comments may be footnoted with Arabic numerals. Because tables are typeset, they need only be submitted typed and formatted, with double-spaced legends. Zeros should precede all decimal points for values less than one. Table headings and format should be consistent; do not use vertical rules.

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Title the list of references "Literature Cited" and include only published works or those actually in press. Citations must contain the complete title of the work, inclusive pagination, full journal title, and the year, month, volume, and issue numbers of the publication. Citations should be double-spaced and listed alphabetically by the senior author's surname and initials. Co-authors should be listed by initials and surname. Where two or more citations have the same author(s), list them chronologically; where both author and year match on two or more, use lowercase alphabet to distinguish them (1979a, 1979b, 1979c, etc.). Authors must double-check all literature cited; they alone are responsible for its accuracy.

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Figures

Figures must be cited in numerical order in the text. Use Times Roman font (upper and lowercase letters) to label within figures. Avoid vertical lettering except for y-axis labels. Zeros should precede all decimal points for values less than one. Figure legends should explain all symbols and abbreviations and should be double-spaced on a separate page at the end of the manuscript. Consider column and page sizes when designing figures. Please note that we do not print graphs in color.

Finally

Authors should proofread the manuscript for typographical errors and double-check its contents and appearance before submission.

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